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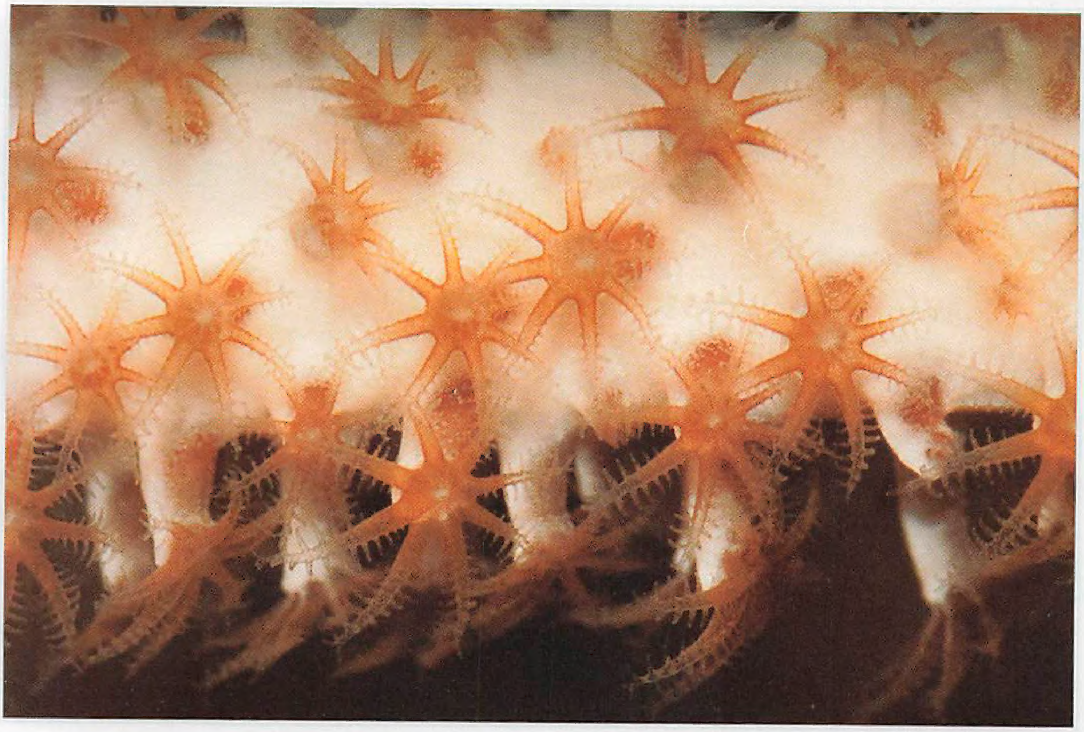

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COVER IMAGE

Zooxanthellae in Philippine ellisellid gorgonians
(Photo by Charles Delbeek, Steinhart Aquarium)

For details see
G.C. Williams, J.C. Delbeek, B. Shepherd, and S. Wolters, pp. 647-648

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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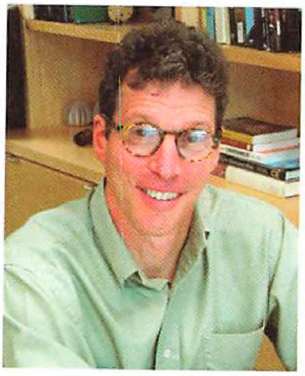
Editorial

Scientific Publications and the California Academy of Science



David P. Mindell
Dean of Science, California
Academy of Sciences

The California Academy of Sciences has been dedicated to scientific discovery and communication since its founding in 1853. This passion is very much alive and well. We inhabit a marvelous new facility, opened in 2008 on the same site in San Francisco's Golden Gate Park that the Academy has called home since 1916, and we have entered a period of significant growth in both scientific productivity and public engagement on scientific issues. The collections of animal and plant specimens, from all regions of the world, have grown to more than 26 million, and these are actively used by Academy Curators and many others in comprehensive studies of the evolution, ecology, and conservation of life on Earth.

During the past year, staff members of the Academy's Research Division have been reviewing how best to respond to technological innovations affecting our communication with colleagues worldwide, with particular emphasis on how we disseminate new information about systematic and taxonomic biodiversity studies. For the last 156 years this was done by means of manuscripts, journals, and books printed on paper. However, scientific publication is increasingly electronic and increasingly open access, meaning, freely available online to anyone. Of course, 'free' is a relative term here, as open access publication costs are borne by authors, grants, and institutional subsidies. This revolution is driven by bottom-up market forces, as electronic publications are generally less expensive to produce and distribute, and by an enlightened and laudable desire to make scientific findings broadly available to researchers and to the public, quickly and without barriers.

Revolutions have consequences, including in this case, raising expectations for unrestricted access by readers as well as fast production, multi-media handling, scientific citation tracking, and broad dissemination by authors and funding agencies. Simultaneously, libraries are being asked to provide more information and resources to more users, despite their shrinking budgets. All of this puts pressure on publishers, and places a premium on the efficiencies that come with larger-scale publishing efforts that can afford to upgrade and promote their online offerings continuously.

Research museums like the California Academy of Science have a long tradition of publishing journals focusing on the discovery and taxonomy of organisms. Many such publications are relatively long and detailed in their comparative analyses, necessarily including more background material and data than found in many journals requiring brevity. Because of their fundamental contribution in naming, describing, classifying, and comparing species, these works are particularly long-lived. This is in contrast to studies published in widely read journals whose general findings, of considerable initial interest, are quickly overturned or supplanted by subsequent research. In light of the extraordinary value of biological diversity to both environmental health and human wellbeing, the importance of taxonomy and systematics publications is as great or greater than ever. The availability of open-access venues for them can and should accelerate their dissemination and their impact on both scientific research and conservation efforts. Unlike publications on paper, electronic publication costs increase little with additional pages and features such as color images, video, sound, and datafiles. A clear strength of online, open access publishing is the enhancement of scientific exchange and innovation, important paths to progress.

In light of all these factors as well as our intent to promote the availability, exchange, and impact of our work, we have, with some reluctance, decided to suspend publication of the *Proceedings* for an indefinite period. In preparing for this occasion, Alan E. Leviton, Editor of the California Academy of Sciences' scientific publications program, and his colleague Michele L. Aldrich, as well as Leviton's former student assistant, Guinevere O.U. Wogan, have prepared a comprehensive indexed bibliography for the Academy's multiple scientific journals dating from 1854 to September 2010. This work is scheduled to appear as Academy *Occasional Paper* 158 and will be published soon after this issue of the Academy's *Proceedings* series. We are deeply indebted to Dr. Leviton for his valuable and excellent work as Editor.

15 September 2010

David P. Mindell
Dean of Science & Research Collections
Research Division
California Academy of Sciences

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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An Outlying *Carlia* Population from Java and Comments on Species Groups within the Genus *Carlia* (Reptilia: Squamata: Scincidae)

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A population of *Carlia* occurs on Pulau Tindjil off the southwest tip of Java, distant from all other populations and species. A set of unique traits identifies the Tindjil *Carlia* as a new taxon; it is described herein. The new species has its closest affinities to populations (*C. peronii, C. spinauris*) living on Timor. Although the latter species has been considered a synonym of the former one, evidence is presented indicating that each name represents a unique species, a lowland and a montane one, respectively. Comparison of *Carlia* species is aided by the establishment of groups of presumed related species; these species groups are named and morphologically defined here.

KEY WORDS: Squamata, Scincidae, *Carlia peronii, Carlia spinauris*, Lesser Sunda Islands, Java, geographic variation, new species, intrageneric relationships, nomenclature.

Carlia, the four-fingered skink, is a moderately diverse genus of Australopapuan lizards. Australia has ~20 species, New Guinea and Papuan shelf islands have ~13 species, and across Lydekker's Line, Wallacea has six described species (Fig. 1). The contrast in diversity in numbers of species and their morphologies is striking on the east and west sides of the Line. The latter aspect is examined in more detail subsequently. In Wallacea, two of the six currently recognized species are the sole members of the *Carlia peronii* species group. This species group and others are defined later; however, the discovery of a population on Tindjil, an island off the southwest coast of Java instigated a re-evaluation of Wallacea *Carlia*. The Tindjil *Carlia* is a distant outlier from other Wallacea *Carlia* populations and has a unique morphology that declares it a different and undescribed species.

Before proceeding with its description, it is necessary to call attention to a nomenclature issue involving its presumed sister species living on Timor. The Timor population of *Carlia* has received two names: *Heteropus peronii* Duméril and Bibron, 1839 and *Lygosoma* (*Leiolopisma*) *spinauris* Smith, 1927. Although the assignment of a name to this population would seem simple, it is not because *H. peronii* is potentially a secondary homonym. This nomenclatural issue is addressed following the description of the Javan species. Evidence indicates that both taxa are valid, thus I use the types of both *H. peronii* Duméril and Bibron and *L. spinauris* Smith for comparison.

A second item requiring attention is the issue of species groups within the genus *Carlia*. Because this topic requires more than a paragraph to delineate the diverse morphologies of the ~40 species of *Carlia*, I note here only that the medium-sized *Carlia* of the Lesser Sundas with their ear-openings completely encircled with pointed lobules represent the *Carlia peronii* species group. I examine intrageneric relationships at the end of this article.

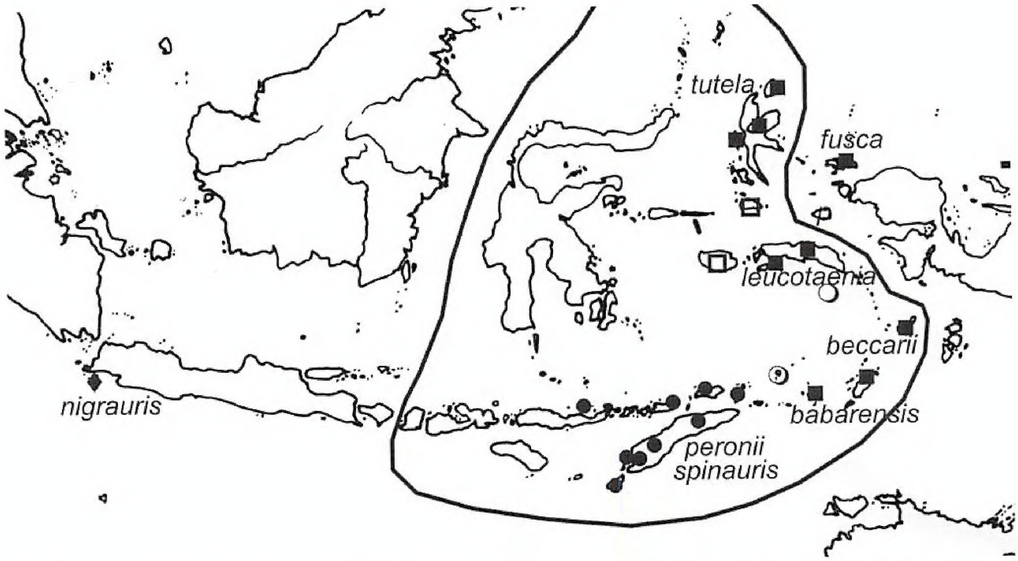

FIGURE 1. Occurrences of species of *Carlia* in Wallacea and Java. Plotting data are given in Appendix 3: Map resources. Wallacea enclosed in solid line. Symbols: diamond, type locality of *C. nigrauris*; circles, *C. peronii* species group members; squares, *C. fusca* species group members; solid symbol, species group assignment certain; open symbol, group assignment uncertain.

The geographic peculiarity of the Tindjil population is striking because of the absence of *Carlia* in the Lesser Sunda Islands west of Flores, and for Flores, *Carlia* is vouchered there only on the offshore island of Pulau Sukur (Fig. 1; Appendix, part 3). The gap from the main cluster of Wallacea *Carlia* is nearly 1800 km. The closest named populations are the Timor *C. peronii* and *C. spinauris*. The Tindjil population is not a member of either of these populations. Other *Carlia* populations occur on Roti, Alor, Wetar, Kisar, and Banda Ids. These populations similarly do not share the morphology of the Tindjil population; they may also represent undescribed species. These unnamed populations are compared also to the Tindjil population (see 'Comparison to other *Carlia*' below).

Carlia nigrauris **Zug, sp. nov.**

Figure 2.

TYPE MATERIAL.— HOLOTYPE: SMF 53916, adult male from Indonesia, Baten Province, Pulau Tindjil (6°58′S 105°45′E), collected by A.M.R. Wegner, 28 June 1955. PARATYPES. SMF 53915, 53917–53922, same locality, date, and collector as holotype; WAM R101496, R101498, Indonesia, Baten Province, Pulau Tindjil (6°58′S; 105°45′E), collected by M. Bangs, 1989; WAM 104927, same locality as preceding, collected by M. Bangs, 4 March 1990. Adult males — SMF 53915, 53917, WAM R101496, R104927, subadult male (immature) – WAM R101498; subadult females (immature) SMF 53919, 53921–53922, juvenile females – SMF 53918, 53920.

DIAGNOSIS.— *Carlia nigrauris* is a member of the *C. peronii* species group and differs from all other group members by the black color of the scales and skin of the ear openings and its perimeter in juveniles and adults. Additionally, *C. nigrauris* averages larger (adult males mean 56 mm SVL) than *C. peronii* and *C. spinauris* (~40 mm SVL) and males have a proportionately longer hindlimb (110% HindlL/TrunkL, 91 and 102% respectively). *C. nigrauris* averages more Dorsal (50), Midbody (33), and 4ToeLm (28) than *C. peronii* and *C. spinauris* (45, 29, 27 and 48, 30, 24, respectively).

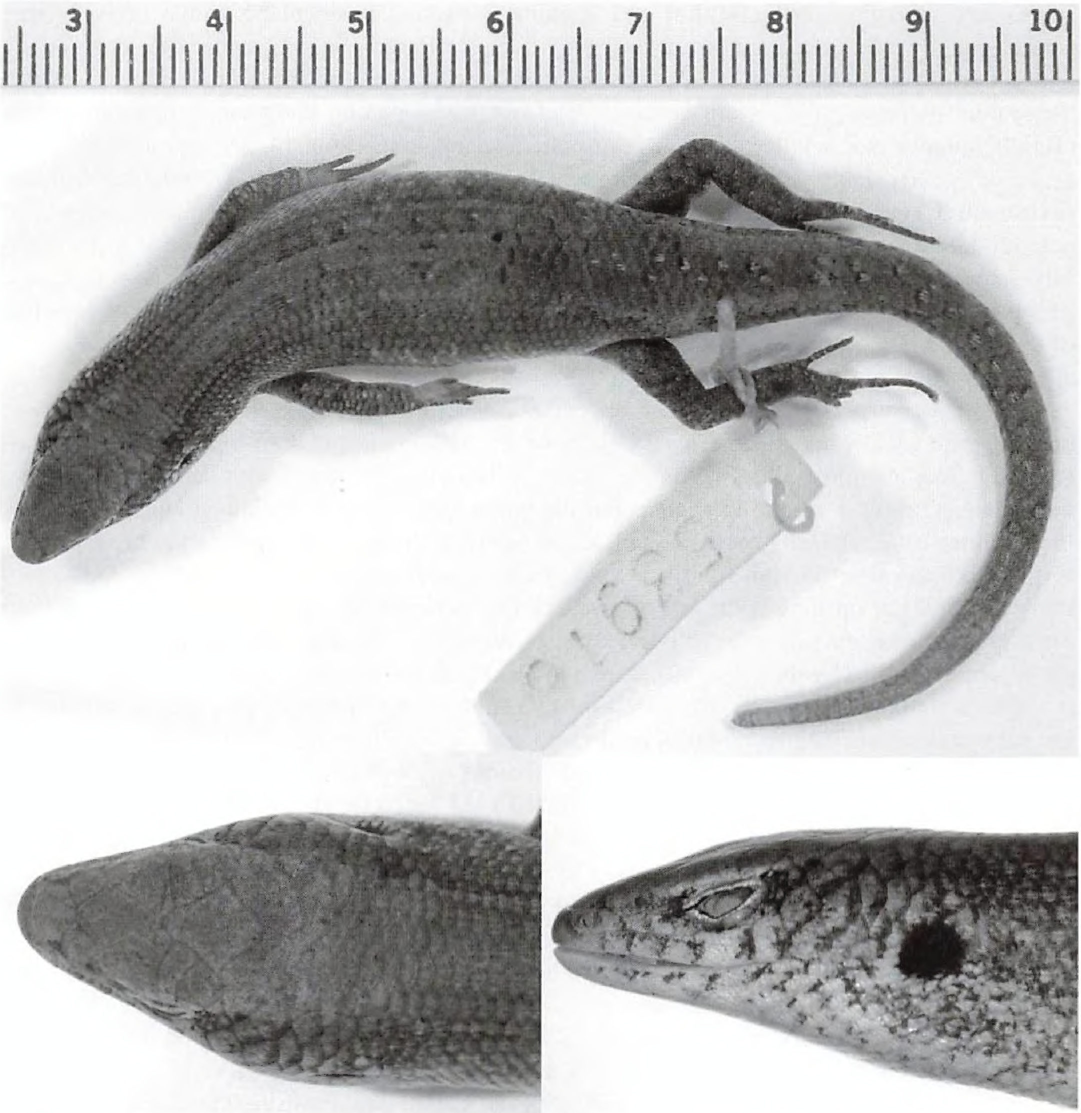

FIGURE 2. The holotype of *Carlia nigrauris* sp. nov., dorsal aspect, preserved, SMF 53916. Bottom row. Dorsal and lateral views of the head of the holotype, respectively.

DESCRIPTION OF HOLOTYPE.— An adult male, 56.4 mm SVL, 64 mm tail length (regenerated, posterior ~third), 25.3 mm TrunkL, 27.4 mm HindlL, 12.8 mm HeadL, 10.3 mm JawW; 4.8 mm SnEye; 2.9 mm SnW; 1.5 mm PalpbD, and 1.6 mm EarD. Scalation right side for bilateral traits: large, flattened pentagonal rostral contacting posteriorly 1st supralabial and large square nasal on each side, and dorsomedially large pentagonal frontonasal; prefrontals large and widely separated on dorsal midline; large frontal and frontoparietal; moderately small triangular interparietal with well-developed parietal eye; pair of large rectangular parietals touching medially behind interparietal; each nasal pierced by large naris; anterior loreal bluntly triangular, higher than wide, and equal-sized to trapezoidal posterior loreal, wider than high; 2 preoculars, lower one largest and abutting large subocular, followed beneath eye and above supralabials by series of small, ovoid suboculars, enlarging posteroventral and forming 7 distinct postoculars; above orbit 4 large supraoculars (Supoc), separated from eyelid by 8 supraciliaries (Supcil); upper eyelid immobile with 8 eyelid rim scales (Eyeld), lower eyelid mobile with 14 eyelid rim scales and with distinct transparent palpebral disc, width subequal horizontal ear-opening diameter; 4 temporal scales (Temp), anterior pair smaller than posterior pair; 7 supralabials (Suplab), 5th largest and beneath center of eye (BlwEye); large semicircular mental followed on each side by 6 infralabials (Inflab), first smallest; round ear-opening, encircled by ~14 acute auricular lobes, ones on anterodorsal and anterior border largest and sharply pointed (AuricN); 51 very weakly tricarinate dorsal scales (Dorsal), anteriormost bilateral pair enlarged as unkeeled nuchal scales; 33 scales rows around middle of trunk (Midbody), 21 smooth ventral lamellae on third finger (3FingL) and 28 smooth lamellae of fourth toe (4ToeL); precloacal scale only slightly larger than immediately anterior ventral scales; all ventral and ventrolateral scales smooth.

Coloration in preservative: Overall appearance is a medium brown lizard from tip of snout onto tail with a white underside. Closer inspection reveals top of head with coppery sheen, laterally head lighter and most scales with posterior edge irregularly bordered with dark brown, edging most distinct on supra- and infralabials; chin and throat bluish ivory with fine reticulation of black lines within scales. Dorsally neck onto tail, scales brown with narrow, diffuse, darker brown edges, forming broad vague middorsal stripe; darker brown dorsolaterally on neck and entire sides of trunk and tail. Ear opening walls and narrow external perimeter black, strikingly so against light brown background grading into the ivory white of the venter. Dorsally, fore- and hindlimbs share the brown of the body with a few dark brown to black specks; ventrally, limbs are white.

DESCRIPTION.— Mensural data based on five adult males (mean±1SD), meristic data on 11 juveniles and adults (median±1SD). A moderately large *Carlia* ranging in adult size from 54 to 58 mm SVL (55.6±1.72) with 21.8–25.8 mm TrunkL (24.1±1.57), 21.0–23.2 mm SnForel (22.4±1.22), and 25.5–27.4 HindlL (26.4±0.76); 12.3–13.7 mm HeadL (13.0±0.58), 8.3–10.3 mm JawW (9.2±0.02), 4.8–5.2 mm SnEye (5.0±0.21), 2.8–3.0 mm SnW (2.9±0.10), 1.5–1.8 mm PalpbD (1.6±0.13), and 1.5–1.8 mm EarD (1.7±0.11). Head and nuchal scales smooth; interparietal always present*; 4 Supoc, 7 Supcil, 8–10 Eyeld (9±0.71), 7 Suplab, 5th BlwEye, and 6 Inflab on each side. Ear opening circular to oblong-vertical, perimeter and upper inner wall with numerous acute auricular lobes, 1–8 (6±2.2) enlarged lobes on anterodorsal and anterior border (AuricN). Trunk scales weakly tricarinate dorsally and laterally, 42–50 Dorsal (50±1.4), 32–35 Midbody (33±0.98). Subdigital lamellae smooth, 18–22 3FingLm (20±1.2) and 26–33 4ToeLm (28±1.9). Without adult females, there is no means to determine whether *C. nigrauris* displays sexually dimorphic in any preceding traits. [*The SMF series of Tindjil *Carlia* was first reported by Mertens in his report (1957a) on the herpetofauna of extreme western Java. The series consisted of 21 juveniles and adults. He reported one individual with interparietal entirely fused with frontoparietal and partially fused in two others. Midbodys were 32–38 and 4ToeLm 26–32 (means 35.1 and 29.4, respectively; my calculations). Mertens recognized that the Tindjil population was distinct but was reluctant to describe them owing to the inadequacy of existing knowledge about '*fuscum*-Formen' [= *Carlia*]. Mertens also presented some generalized color notes on the preserved specimens.]

Coloration is summarized in the subsequent Intraspecific Variations section.

DISTRIBUTION.— Known presently only from Pulau Tindjil [Tinjil, an alternate spelling] lying just off the southwest coast of Java (Fig. 1).

ETYMOLOGY.— The specific name derives from the Latin *nigra* (feminine) for black and *auris* (f.) for ear in reference to the color of the wall of the ear-openings and the external perimeter of adjacent head scales.

INTRASPECIFIC VARIATION.— In preservative, the colors of all life stages are muted and likely the striped appearance of juveniles and subadult females is brighter and bolder in life and the brown of adults males has an iridescent sheen. Data on living individuals are not available.

The two SMF adult male paratypes do not differ strikingly from the holotype; both show the overall brown on the top of the head and remainder of trunk and tail. Ventrolaterally, their heads have the variegated light and dark pattern and the black walls and perimeter of the ear-openings make them appear larger than they are. The venters are ivory white with dark gray edging on posterior chin and anterior throat scales yielding a dusky longitudinal striping on throat. The largely regenerated tail of SMF 53915 appears orangish brown, particularly ventrally. The largest subadult female (WAM R101498) of the type series was too dehydrated to yield reliable coloration, similarly for the two adult WAM males.

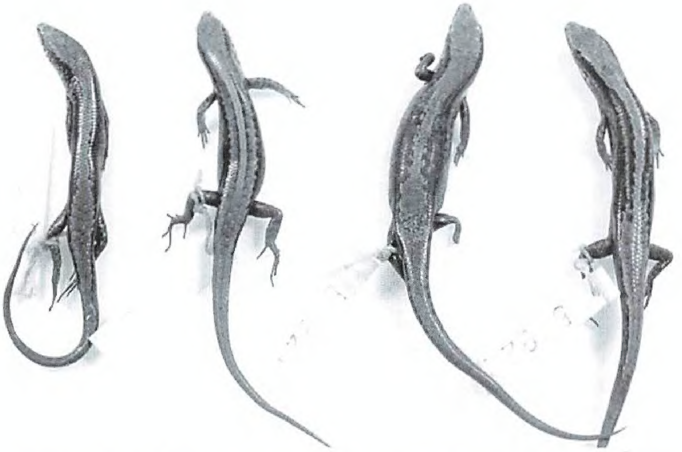

FIGURE 3. The dorsal coloration of juvenile and subadult female *Carlia nigrauris*, preserved. From left to right: SMF 53918, 53929, 53921, 53922.

The smallest paratypes (SMF 53918, 53920; both ~39 mm SVL) are juvenile females. Both are boldly striped although each in a somewhat different pattern. They share a broad middorsal stripe from the rear of the neck to the sacral area. This light stripe is bordered laterally by darker brown extending to the ventrolateral surface of the trunk, gradually becoming lighter toward the venter. In SMF 53918 (Fig. 3), the middorsal stripe is continuous with the coppery green top of the head and the dusky greenish brown of the sacral area and anterior half of the tail. On the neck and trunk, the stripe is glossy green muted by pairs of diffuse brown bars on each stripe scale. Laterally on neck, trunk and base of tail, the background color is dark brown and nearly black immediately adjacent to the middorsal stripe. On closer inspection, the lateral brown background is speckled with flecks (usually about half of a scale) of lighter brown or green; the green flecks are more numerous than the brown ones. The loreal and temporal areas of the head are predominantly brown; the upper and lower lips are green and brown barred. The black of the ear is confined to the internal walls. The venter is bluish ivory with the same dark scale marking as on the chin and throat scales of the adults. Fore- and hindlimbs are two-toned dorsally with the proximal portion dark brown matching the dorsolateral trunk color, distal half and foot medium brown; some lighter flecks. Ventrally, limbs are whitish like the trunk venter.

In SMF 53920, the middorsal stripe is slightly narrower than in the former juvenile and is beige from shoulder to sacrum, where the stripe disappears by merging with the parasagittal stripes into the dusky tan dorsal surface of the tail. Anteriorly from mid-neck, the dorsal surface is light brown to the tip of the snout. The middorsal stripe on rear of neck and trunk is narrowly edged with dark brown; a broad coppery brown stripe lies parasagittally on each side. Dorsolaterally the surface is dark brown from behind the eye to the base of the tail. The dark brown gradually lightens ventrolaterally as it merges into the bluish ivory venter. The sides of the head and ear-openings are as in the other juvenile. Limbs are also similar to the former juvenile.

The three SMF females are similar-sized (44–47 mm SVL) subadults (slightly enlarged ovarian follicles, oviducts strap-like). All three retain the juvenile coloration, most similar to SMF

53920, but the middorsal and parasagittal light stripes are narrower owing to the expansion of the dark brown border between them. The side of head, neck, and trunk are as in the juveniles. The black surface is confined to the walls of the ear-opening. The venters are bluish ivory with diffuse dark striping on chin and anterior neck.

COMPARISON TO OTHER *CARLIA*.— This comparison examines only geographically adjacent taxa and populations, i.e., Wallacea and islands of the New Guinea shelf adjacent to Lydekker's Line. Comparison to more distant taxa and populations is available in the subsequent discussion of species groups within the genus *Carlia*.

Currently, there are six named populations of *Carlia* within Wallacea (Fig.1): *C. babarensis* (Babar and Tanimbar); *C. beccarii* (Kai); *C. leucotaenia* (Ambon and Seram); *C. peronii* (Timor); *C. spinauris* (Timor); and *C. tutela* (Halmahera, Morotai, Ternate). Unassigned *Carlia peronii* group populations are vouchered by adequate samples from several other Wallacea islands (Alor, Kisar, Roti, Pulau Sukur, Banda) to permit comparison with *C. nigrauris*. These unassigned populations might represent new species or representatives of *C. peronii* or *C. spinauris*; however, that analysis requires more recently collected specimens with color notes and/or images of vouchered living specimens. Recent and ongoing fieldwork in Timor-Leste likely will provide an opportunity for such a detailed analysis by those fieldworkers.

Wallacea species (*C. babarensis*, *C. beccarii*, *C. leucotaenia*, *C. tutela*) have been assigned to the *C. fusca* species group (Zug 2004). Even though ear-shape can be altered in preservation, its oblong oblique or vertical orientation in the *fusca*-group taxa is strikingly different from the usual circular ear-opening of the *peronii*-group taxa. Additionally the rim of the latter group is completely encircled with acute auricular lobes, distinctly pointed on anterior and anterodorsal edge, contrasting with the blunter lobes confined to the anterior and anterodorsal border in the *fusca*-group taxa. These four *fusca*-group taxa bracket, but do not overlap, adult male SVL with *C. nigrauris* (54–58 mm): *C. babarensis* 45–51 mm; *C. beccarii* 65-80 mm; *C. leucotaenia* 43–53 mm; *C. tutela* 41–54 mm. All five taxa share similar body proportions, although hindlimbs of *C. beccarii* are longer than in the other taxa, i.e., 50–59% HindlL/SVL to 39–54% for others. Not as striking, trunk length of *C. nigrauris* (40–45% TrunkL/SVL) lies in the lower half of the range of the *fusca*-group members (39–51%).

Among the *peronii*-group, *C. nigrauris* is the largest member with all other populations distinctly smaller (Table 1). The largest males in the Kisar and Banda samples are 47 mm SVL. The Timor-WAM and Banda samples show size dimorphism between adult females and males; these two samples and the Alor one (not size dimorphic) are the only ones with adequate numbers of females and males to test for dimorphism. Aside from the overall size difference between *C. nigrauris* and its *peronii*-group relatives, body proportions are generally similar (comparison confined to males). Among adults, *C. nigrauris*, Alor males, Kisar males, and Banda females and males have proportionately longer hindlimbs. Among *Carlia* and other skinks, females regularly have longer trunks than males; this dimorphism is evident in the larger *peronii*-group samples, but statistically significant only in the Banda sample.

In scalation, *C. nigrauris* is a typical *fusca*- and *peronii*-group taxon, that is scalation traits are little different (ranges overlap) among the species. The exception is the auricular lobe trait. I note here the low variability of scalation traits in all samples, even in the combined juvenile and adult samples. Coefficients of variation (*v*) range between 3 and 9% for mensural traits (adult only samples) and 3–9% for the scalation and proportions in both adult-only and combined juvenile-adult samples.

Among the *peronii*-group samples, Dorsal, 3FingLm, 4ToeLm, and DorsKN (Table 2) offer the greatest intersample difference and potential evidence of possible regional differentiation. In

TABLE 1. Summary of variation in select mensural characters in adult samples of the *Carlia peronii* species group. Mean ± 1 standard deviation, range, and statistically significant dimorphism * (Student's t $p \leq 0.05$); sample size in brackets; species assignment in parentheses.

Locality		SVL	TrunkL/SVL	HindlL/Trunkl	HeadL/SVL	EarD/Headl
Java-Tindjil	[5 ♂]	55.6±1.72	0.43±0.019	1.10±0.0.62	0.23±0.008	0.13±0.005
(*nigrauris*)		54.3–58.3	0.40–0.45	1.03–1.18	0.23–0.25	0.12–0.14
Timor						
H. peronii D&B	[1 ?]	32.3	0.45	1.02	0.24	0.13
(MNHN 3037)						
L. spinauris Smith	[1 ♂]	41.3	0.46	0.91	0.2	0.17
(BMNH 1946.8.17.58)						
Timor-WAM	[11 ♂]	39.1±1.82*	0.45±0.021	0.96±0.066*	0.23±0.007*	0.14±0.017
		34.6–40.8	0.43–0.50	0.86–1.05	0.21–0.24	0.11–0.17
	[11 ♀]	37.0±1.57*	0.47±0.027	0.85±0.063*	0.21±0.006*	0.14±0.016
		34.7–39.9	0.43–0.51	0.78–0.98	0.21–0.22	0.12–0.17
Roti	[1 ♂]	41	0.43	1.12	0.22	0.11
(unassigned)	[4 ♀]	38.0±1.10	0.45±0.025	0.87±0.031	0.21±0.007	0.12±0.007
		36.4-38.0	0.42-0.48	0.84-0.90	0.21-0.22	0.11-0.13
Alor	[7 ♂]	43.2±1.74	0.43±0.028	1.06±0.084*	0.23±0.006*	0.13±0.011
(unassigned)		40.0–45.0	0.40–0.48	0.90–1.15	0.23–0.24	0.12–0.15
	[8 ♀]	42.1±1.17	0.47±0.034	0.89±0.088*	0.22±0.006*	0.14±0.011
		39.4–43.0	0.42–0.51	0.73–1.06	0.21–0.22	0.11–0.15
Kisar	[7 ♂]	46.0±1.88	0.45±0.012	1.04±0.082	0.23±0.008	0.13±0.005
(unassigned)		42.2–47.4	0.44–0.47	0.94–1.17	0.22–0.24	0.12–0.14
	[2 ♀]	40.0±0.07	0.49±0.026	0.95±0.085	0.22±0.009	0.13±0.005
		39.9–40.0	0.47–0.50	0.89–1.05	0.21–0.23	0.12–0.13
Other outliers						
Pulau Sukur	[2 ♂]	40.7±0.50	0.50±0.020	0.93±0.079	0.22±0.015	0.15±0.015
(unassigned)		40.3–41.0	0.49–0.52	0.87–0.99	0.21–0.23	0.14-0.16
	[3 ♀]	39.7±0.65	0.52±0.019	0.84±0.053	0.22±0.011	0.16±0.007
		39.1–40.4	0.50–0.54	0.78–0.87	0.21–0.23	0.16–0.17
Banda Ids.	[7 ♂]	44.8±1.45*	0.42±0.013*	1.17±0.043*	0.24±0.005*	0.13±0.009
(unassigned)		42.7–46.6	0.40–0.43	1.09–1.23	0.24–0.25	0.12–0.14
	[6 ♀]	42.9±1.58*	0.46±1.380*	1.01±1.604*	0.23±0.001*	0.12±0.378
		41.5–45.8	0.43–0.50	0.97–1.06	0.22-0.23	0.10–0.14

Dorsal, the overall range is 45 to 55 scale rows with Alor possessing the highest average (53) and Timor-WAM the lowest (47). 3FingLm ranges 15 to 22; most samples average 17 or 18, but *C. nigrauris* (20) and Banda (21) have distinctly higher means. A similar pattern occurs for 4ToeLm with 23 and 24 the most frequent means, and *C. nigrauris* and Banda adult males with means of 29. All *peronii*-group samples show striations or weak keeling on dorsal trunk scales. The most common DorsKN is tricarinate. Some individuals of Timor-WAM, Roti, and Alor have a mix of bicarinate and tricarinate scales on the dorsal and upper lateral trunk; tricarinate scales are the

TABLE 2. Summary of variation in select meristic characters in samples of the *Carlia peronii* species group. Median ± 1 standard deviation, range, and statistically significant dimorphism* (Student's t p≤0.05); sample size in brackets; species assignment in parentheses.

Locality		Dorsal	Midbody	3FingLm	4ToeLm	DorsKN
Tindjil	[5 ♂]	49±1.58	33±0.55	20.5±0.96	29±2.07	3±0.0
(*nigrauris*)		47–51	33–34	20–22	28–33	
	[11 juv & ad]	50±1.37	33±0.98	20±1.20	28±1.91	3±0.0
		47–51	32–35	18–22	26–33	
Timor						
(*peronii*)	[?]	45	29	19	27	2
(*spinauris*)	[1 ♂]	48	30	19	24	3
Timor -WAM	[11 ♂]	47±1.3	31±0.79	17±1.22	23±1.83	3±0.47
		45–49	30–32	15–19	19–25	2–3
	[11 ♀]	48±0.82	30±1.43	17±1.44	24±1.29	3±0.41
		46–48	28–32	15–20	21–25	2-3
Roti	[8 ♀]	51	33	17	24	2
(unassigned)		46–51	32–34	15–20	22–26	2-3
	[8 juv & ad]	49.5±1.60	32±0.76	17.5±1.60	23.5±1.28	2±0.46
		46–51	32–34	15–20	22–26	2–3
Alor	[7 ♂]	51±1.35*	34±1.38	18±0.98	24±1.95	3±0.0
(unassigned)		49–51	1–35	15–20	22–27	
	[8 ♀]	53±1.13*	33.5±1.17	17±1.20	23.5±2.39	3±0.35
		51–55	32–35	16–20	21–27	2–3
Kisar	[7 ♂]	50±1.35	33±0.79	18±1.16	25±1.13	3±0.0
(unassigned)		48-52	31–33	16–19	24–27	
	[9 juv & ad]	50±1.74	33±1.23	18±1.05	26±1.27	3±0.0
		48–54	30–34	16–19	24–28	
other outliers						
Pulau Sukur	[2 ♂]	50±1.41	33±0.0	18.5±0.71	25±2.83	3±0.0
(unassigned)		49–51	--	18–19	23–27	
	[11 juv & ad]	51±1.0	33±0.75	18±0.93	24.5±1.43	3±0.0
		49–53	32–34	17–20	22–27	
Banda Ids.	[7 ♂]	46±0.95*	33±1.51	21±0.54	29±1.38	0±1.60
(unassigned)		45-48	30–34	21–22	26–30	0–3
	[6 ♀]	48.5±0.98*	32.5±0.82	21±1.17	28.5±0.55	1.5±1.64
		47–49	32–34	19–22	28–29	0–3

most abundant, and infrequently bicarinate scales dominate. Individual Banda *Carlia* has smooth or weakly tricarinate dorsal scales.

Greer (1976) described the coloration of the *H. peronii* holotype as having a narrow light dorsolateral stripe from ear to end of trunk, a narrow midlateral light stripe from ear to at least midtrunk, and the two light stripes enclosed a broader dark brown stripe with a few tiny light spots on each side, and dorsally olive brown with a scattering of small brown spots on the edges of some dorsal scales. My notes on the type agree with Greer's description of lateral coloration and additionally a narrow dark middorsal stripe. Smith's description (1927) of *C. spinauris* is brief: dorsum dark brown with indistinct light dorsolateral stripe bordered below with black (width of the black is not given), and venter is white with throat black spotted. A specimen (RMNH 7941) from Semau (island opposite Kupang) had a 'fusca" brown dorsum with slight peppering of dark brown, dorsolateral light stripe continuous from eye to anterior quarter of trunk, no midlateral light stripe and dusky brown sides from ear to inguen. Alor juveniles and adults have a brown dorsum from snout onto tail with black speckling (dark scale edges) on trunk, moderately broad dorsolateral light (tan) stripe from snout onto tail (ontogenetically disappears from snout to eye, then eye to ear, and become more diffuse but still distinct on neck and trunk in adults); laterally brown, dark brown from eye to trunk just behind forelimb, thereafter brown same as dorsum; laterally temporal area and neck spotted with white; venter ivory and throat with narrow black stripping. Color slides (R. How) were available for a living specimen each from Wetar (WAM R117553, adult male) and Kisar (WAM R117487, adult male). The Wetar male was brown from head to base of tail, brassy anteriorly becoming lighter, somewhat coppery on posterior half of trunk; laterally head brown, supra- and infralabials white with black edges, brown and white mottling continues on neck to axilla; side of trunk golden beige with band of bright orange from shoulder to hindlimb, lighter on posterior half and side of tail orangish; sides of throat with dark and light striping. Inside of ear-opening appeared dark. The Kisar male similarly colored although less bright laterally on trunk and lateral trunk band a subdued coppery orange; dorsolaterally neck unicolor dark brown and more diffused dark and light mottling below, white spot behind ear. None of these colorations match the pattern of *C. nigrauris*. Timor *C. peronii* and *C. spinauris*, and the Alor population display a distinct dorsolateral light stripe from ear to inguen. The Wetar and Kisar populations lack the dorsolateral light stripe (at least in adult males) and any indication of dark brown on sides of trunk.

NATURAL HISTORY.— Mertens (1957a) included no natural history information. Notes with some WAM specimens mentioned that they were found on ground as is typical for *Carlia*.

TIMOR *CARLIA* — NOMENCLATURAL REVIEW

Duméril and Bibron (1839) described *Heteronotus peronii* from a specimen with the locality data of "Ile de France" [= Mauritius], an erroneous licality. The description is adequate to recognize the specimen as a four-fingered skink. When Boulenger (1887) published his catalog of lizards, he reassigned *H. peronii* D&B and a multitude of other skinks to the genus *Lygosoma*. He specifically included three of De Vis's Queensland taxa (*Myophila vivax* DV 1884, *Heteropus lateralis* DV 1885, *H. blackmanni* DV 1885) as synonyms of *H. peronii*. It is not known whether Boulenger examined the type of *H. peronii* D&B. Boulenger also assigned *Seps peronii* Fitzinger 1826 (an unrelated Australian reduced-limbed taxon) to *Lygosoma* thereby creating a homonymy with *Lygosoma peronii* (D&B) as a secondary homonym. Boulenger did not address this homonymy; indeed, he presented two *Lygosoma peronii* species accounts in his Catalog (i.e., *Lygosoma peronii* (D&B) account #82, page 286 and *Lygosoma peronii* (Fitzinger) #134, page 326). The Strickland nomenclatural code was in effect when Boulenger published his Catalog, and that code recognized the necessity of replacing secondary/junior homonyms with a new name. Boulenger offered no replacement name for *H. peronii* D&B, nor has anyone else since its creation as a homonym.

De Rooij (1915) did not list any four-fingered *Lygosoma* from Timor. This absence re-enforced the persistence of D&B's incorrect type-locality for *H. peronii* and de Rooij's acceptance of *L. peronii* (D&B) as a member of the Australian herpetofauna and outside the area of her treatise.

In 1927, Malcolm Smith described the four-fingered skinks that he had collected in the mountains of Timor as *Lygosoma* (*Leiolopisma*) *spinauris* Smith 1927. Because he had no reason to suspect that *L. peronii* (D&B) derived from Timor, he was unaware that a Timor population had a scientific name.

In 1952, Mittleman resurrected *Carlia* Gray for the four-fingered Australopapuan skinks and *Hemiergis* Wagler for the group of reduced-limbed (four digits or fewer on fore- and hindlimbs) Australian skinks. Mittleman also included a list of species for all his resurrected genera, and specifically noted in the introduction to this list that he considered all listed species to be "distinguishable racial entity."(Mittleman 1952:21.) This action removed the homonymy and re-established *Carlia peronii* (D&B) and *Hemiergis peronii* (Fitzinger) as valid and separate taxa.

In 1953, Mitchell reviewed the status of the four-fingered skinks of Australia. He continued the use of *Leiolopisma*, because either he was unaware of Mittleman's generic reorganization or his manuscript was in press when Mittleman's synopsis appeared. Because *L. peronii* (D&B) was assumed to be an Australian *Carlia* and related to or synonymous with *L. vivax* (De Vis), he called attention to the situation by stating "[*peronii*] suppressed as a homonym in the genus *Lygosoma*." (Mitchell 1953:85.) His action was appropriate and potentially suppressed the use of *peronii*, because the nomenclatural code then in effect and the subsequent edition defined a secondary homonym as an identical species group name established for different nominal taxa subsequently brought together in the same generic name group. The younger name is the secondary homonym and invalid.

In 1976, Greer examined the type of *Heteropus peronii* D&B and recognized that it was most similar to *Carlia spinauris* (Smith). Following a detailed morphological comparison of *H. peronii* with Smith's type specimens of *L. spinauris*, he concluded that the latter was a synonym of the former. He did not address the issue of the *peronii* homonymy. Under the nomenclatural code then in effect, he could have declared *H. peronii* D&B invalid owing to Boulenger's 1887 creation of a secondary homonym. Instead, he accepted the name as a senior synonym for the Timor *Carlia*, and further demonstrated that D&B's 'Ile de France' type locality was incorrect and reassigned the type-locality to Timor. He examined the itinerary of Peron and suggested that the MNHN type likely derived from "the principal harbor and town of Timor" [= Kupang] and not from Semau [island opposite Kupang]. If we accept this origin [and there is no compelling reason to reject it], this origin of the holotype of *H. peronii* D&B has important ramifications for the assignment of names to Timor populations.

Mittleman's resurrection of *Carlia* and Greer's failure (intentional or otherwise) to address the *peronii* homonymy create a potential nomenclature quagmire if we follow the "letter of the" Code that was in force when Mitchell noted the homonymy. Mitchell, however, did not propose a replacement name, and his nomenclature comment occurred a year after Mittleman eliminated the homonymy by resurrection of *Carlia*. Further, the actions of Mittleman and Greer re-established the regular use of the name *Carlia peronii* (D&B) in the herpetological literature. The absence of a previous examination and the resolution of this nomenclatural matter allow me to propose the validity of *Carlia peronii* (Duméril and Bibron) under Article 59.2 of the present Code (1999, ICZN, 4th ed.).

As noted earlier, I consider both *C. peronii* (D&B) and *C. spinauris* (Smith) as valid Timor species, the former a lowland species and the latter a montane one, based on the type localities of their holotypes. The situation is potentially more complex if Hinrich Kaiser's assessment (*in litt.*, December 2009) of four species in Timor-Leste is correct; however, both named species derive from west Timor, and one of his challenges will be to determine whether one or both western Timor *Carlia* also occur in Timor-Leste.

TIMOR *CARLIA* — MORPHOLOGY OF *C. PERONII*

The Timor-WAM sample derives from Kokabis (10°11′S 123°46′E), a small village ~25 km east of Kupang in an undulating and largely agricultural landscape (Google Earth, 28 Jan. 2010 image), and one Kupang specimen. This sample offers an opportunity to characterize *Carlia peronii* as a population instead of as a single immature individual. This characterization is based on an assumption of the accuracy of the type locality of *H. peronii* D&B. As noted in the preceding nomenclatural review, *H. peronii* D&B and *L. spinauris* Smith are available and represent different populations owing to their type localities. The former derives from a lowland locality, i.e., vicinity of Kupang, the major port of Timor and the only Timor location visited by Peron (Greer 1976). The holotype of *L. spinauris* was personally collected by M. Smith and his wife at Lelogama, which he (Smith 1927) describes as wooded hilly area (750 m elevation). Thus south (or west) Timor appears to have two species of *peronii*-group *Carlia*, an upland and a lowland one. Of the Timor samples available, I have analyzed only the WAM specimens; the following characterization of *Carlia peronii* (D&B) is based on that sample.

Carlia peronii is a moderately small skink, ranging in adult size from 35 to 41 mm SVL (♂ 39.1±1.82, 34.6–40.8; ♀ 37.0±1.57, 34.7–39.9) with 15.0–19.9 mm TrunkL (♂ 17.7±0.95, 16.1–19.3; ♀ 17.4±1.46, 15.0–19.9), and 14.7–18.1 HindlL; (♂ 17.0±0.88, 15.7–18.1; ♀ 14.7± 0.95, 13.0–15.7); 7.4–9.3 mm HeadL (♂ 8.9±0.44, 7.9–9.3; ♀ 7.9±0.32, 7.4–8.4), 1.0–1.3 mm PalpbD (♂ 1.2±0.1.0–1.3; ♀1.1±0.10, 1.0–1.3), and 0.9–1.4 mm EarD (♂ 1.2±0.13, 1.0–1.4; ♀ 1.1±0.11, 0.9–1.3). Body proportions Timor-WAM in Table 1, scalation in Table 2. Head and nuchal scales smooth; interparietal always present; prefrontal large but separated by rostral and frontonasal in contact, 4 Supoc, 7 Supcil (rarely 6 or 8), 7–10 Eyeld (9±0.91), 7 (rarely 6) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening circular or nearly so, perimeter and upper inner wall with numerous acute auricular lobes, 1–9 (5±2.2) enlarged lobes on anterodorsal and anterior border (AuricN). Trunk scales weakly tricarinate and/or bicarinate dorsally and laterally (65% tri, 27% mixed, 8% bi), 45–49 Dorsal (47.5±1.10), 28–32 Midbody (30.5±1.13). Subdigital lamellae smooth, 15–20 3FingLm (17±1.31) and 19–25 4ToeLm (23.5±1.59), some digits with pre-penultimate and penultimate lamellae creased (may reflect specimen dehydration rather than real state. Adult sample sexually dimorphic (Student's t $p \leq 0.05$) in SVL, HindlL, HeadL, PalpbD, HindlL/SVL, HindlL/TrunkL, HeadL/SVL, and Supcil. Aside from Supcil, 4ToeLm and shape of ear-opening, the preceding characterization matches Greer's (1976) redescription of the holotype of *H. peronii* D&B. My lower by one 4ToeLm likely represents a difference in defining the first proximal lamella; the first one for me is the first lamella wider than long and in contact with dorsal digit scales. Ear-opening shape is strongly dependent upon condition at time of preservation; any dorsoventral compression or bending of the head will alter the original condition.

Greer (1976) noted that the *H. peronii* holotype had a narrow light dorsolateral stripe from ear to end of trunk and a narrow midlateral light stripe from ear to at least mid trunk; the two light stripes enclosed a dark brown stripe with a few tiny light spots. These data on coloration can be expanded by an examination of the frequency of striping. My wife and I recorded a set of five pattern traits in a large sample of adult Timor-WAM specimens ($n = 37$, 18 ♂ 19 ♀):1) chin-throat scales — no black edges, little to moderate black edging, most scales black edged; 2) dorsolateral light stripe on neck — absent or present; 3) lateral light stripe on neck – absent or present; 4) dorsolateral light stripe on trunk — absent or present; 5) lateral light stripe on trunk — absent or present. Only one female lacked black-edged scales on the throat, 13 females (68%) had moderate amount of edging, and five had most scales black edged. In contrast, 15 males (83%) had most scales black edged and only three with moderate edging. Sexual dimorphism also occurred in levels of the dorsolateral and lateral light striping. All females retained neck and trunk dorsolateral stripes, and all females possessed lateral stripes on the neck and 16 (84%) had lateral stripes on the trunk. All males had a dorsolateral stripe on the neck but only three (17%) retained the dorsolateral stripe on the trunk. Most males (83%) had the lateral stripe on the neck, but none had a lateral trunk stripe. Males and females had similar frequencies of DorsKN; most individuals were tricarinate (67% ♂ 68% ♀); a few individuals of each sex were mixed bi- and tricarinate; and two females and one male were bicarinate.

CARLIA MORPHOLOGY — SPECIES GROUPS

The last quarter of the 20th century saw the Australopapuan four-fingered skinks *Carlia* going from a relatively obscure and low diversity group with 12 species (Mitchell 1953) to nearly 40 species now and others await description. First, Storr (1974) reviewed the populations of Western Australia and the Northern Territory, recognizing four new species and two existing ones. On the opposite side of the continent, Covacevich and Ingram in a series of research articles, ending with their 1989 review (Ingram and Covacevich 1989) added five new taxa, recognizing a total of 21 Australian species (including three species recently transferred to *Liburnascincus*). Zug's review (2004) of the New Guinean *Carlia fusca* resulted in a fissure of this taxon into 19 species, including six new ones and eight resurrected ones; further four differentiated populations were not described. With this increase in diversity, interest in their interspecific relationships grew, and Stuart-Fox (1998; and subsequently Stuart-Fox et al. 2002) performed a phylogenetic analysis with mtDNA. Unfortunately, the results (strict consensus of best MP and ML tree) showed poor resolution of species relationship with the majority (16 of 19) of the taxa arising from a midlevel polytomy. A few taxa were linked: (*C. "fusca," C. longipes*); (*rhomboidalis*, southern *rubrigularis*); (*rostralis, vivax*); (*johnstonei, triacantha*); (*munda, rufilatus*); and at lower levels, all *Lygisaurus* including *C. parrhasius*, (*gracilis* (*bicarinata, pectoralis*)), and (*coensis, mundivensis*).

Zug (2004) attempted a phylogenetic analysis with a set of 21 external morphological characters; his results also yielded a largely unresolved tree. Three species pairs and one triplet suggested some relationships: (*dogare, vivax*); (*jarnoldae, pectoralis*); (*coensis, scirtelis*); (*munda* (*gracilis, rufilata*)). More recently, Dolman and Hugall (2008) increased the molecular data, eliminating the polytomy and obtained a number of well-supported clusters (clades) of taxa. Critically, their data showed a single basal dichotomy between the long-limbed, rock-dwelling '*Carlia*' (*coensis* (*mundivensis, scirtetis*)) and all other '*Carlia*.' This latter group also showed a sister group relationship to the *Lygisaurus-Carlia* clade. They resurrected *Liburnascincus* for the rock-dwelling taxa and re-established *Lygisaurus*. The branching within *Carlia* is reasonably robust and yields numerous clades. Donnellan and colleagues (2009) examined relationships within the Australian populations of the *Carlia fusca* complex (= species group) with a molecular, karyotypic, and morphological data set. Although they emphasized the *fusca* group population relationships, they also included an assortment of other *'Carlia'* and confirmed that *Liburnascincus* and *Lygisaurus* were valid clades. Further their data revealed that the Australian *fusca* group member *Carlia longipes* contained at least three recognizable species and supported the phylogenetic unity of the *fusca* species group.

I find it useful to identify species groups within *Carlia* to examine the origin, divergence, and biogeography of the various species. Dolman's and Hugall's Maximum Parsimony tree (2008: fig. 2) provides putative clades on which to construct group content and definitions. Their MP tree contains three major clades (*Liburnascincus* (*Lygisaurus Carlia*)). Bootstrap support for the sister group bifurcation of *Liburnascincus* and the other two genera and for the linkage of *Liburnascincus coensis*, *L. mundivensis*, and *L. scirtetis* is 100%. Bootstrap support for the *Lygisaurus* and *Carlia* is less strong but still significant (70%). The monophyly of the 17 Australian and three New Guinea *Carlia* of their data set is quite robust (97%). Subsequent bifurcations within *Carlia* are weakly supported until near the crown-group level. The two strongest supported clades are the *fusca* group (*longipes*, *mysi*, and an undescribed S Highlands PNG population) and the *rhomboidalis* group (*rhomboidalis*, *rubrigularis*). Other clades are less robust (bootstrap values <50%); nonetheless, the MP clades suggest the following groups: *vivax* group (*vivax* (*dogare*, *rostralis*)); *tetradactyla* group (*amax*, *tetradactyla*); *triacantha* group (*rufilatus* (*johnstonei*, *triacantha*)); *munda* group (*munda*, *pectoralis*); *bicarinata* group (*storri* (*bicarinata*, *schmeltzii*)); *gracilis* group (*gracilis*, *jarnoldae*). Definitions for these species groups are available in Appendix 4.

Placement of some *Carlia* species within groups rests solely on morphology, because these taxa have not been included in molecular phylogenetic analysis. Dolman and Hugall (2008) sampled broadly among the Australian species and only *C. rimula* was missing from their analysis.

Carlia rimula is a small skink (mean ~32 mm SVL, max. 39 mm) from east-central Cape York Peninsula and the smallest of the currently recognized *Carlia*. Its character states are a broad mix of those defining the species group, therefore they do not allow a convincing assignment to any of the species groups, not even to those groups containing members of strikingly divergent morphologies. Is *C. rimula*, like *C. parrhasius*, incorrectly placed in *Carlia* or will it prove to be a basal divergence like the *gracilis* group?

TABLE 3. Geographic arrangement and species group assignment of the currently recognized species of genus *Carlia*.

Australian Taxa [20]	
Carlia amax	*tetradactyla* species group
Carlia dogare	*vivax* species group
Carlia gracilis	*gracilis* species group
Carlia jarnoldae	*gracilis* species group
Carlia johnstonei	*triacantha* species group
Carlia longipes	*fusca* species group
Carlia munda	*munda* species group
Carlia pectoralis	*munda* species group
Carlia quinquecarinata	*fusca* species group
Carlia rhomboidalis	*rhomboidalis* species group
Carlia rimula	not assigned
Carlia rostralis	*vivax* species group
Carlia rubrigularis	*rhomboidalis* species group
Carlia rufilatus	*triacantha* species group
Carlia schmeltzii	*bicarinata* species group
Carlia sexdentata	*fusca* species group
Carlia storri	*bicarinata* species group
Carlia tetradactyla	*tetradactyla* species group
Carlia triacantha	*triacantha* species group
Carlia vivax	*vivax* species group
New Guinea Taxa [13]	
Carlia aenigma	*fusca* species group
Carlia ailanpalai	*fusca* species group
Carlia aramia	*fusca* species group
Carlia bicarinata	*bicarinata* species group
Carlia bomberai	*fusca* species group
Carlia caesius	*fusca* species group
Carlia diguliensis	*fusca* species group
Carlia eothen	*fusca* species group
Carlia fusca	*fusca* species group
Carlia luctuosa	*fusca* species group
Carlia mysi	*fusca* species group
Carlia pulla	*fusca* species group
Carlia storri	*bicarinata* species group
Wallacea Taxa [7]	
Carlia babarensis	*fusca* species group
Carlia beccarii	*fusca* species group
Carlia leucotaenia	*fusca* species group
Carlia nigrauris	*peronii* species group
Carlia peronii	*peronii* species group
Carlia tutela	*fusca* species group
Carlia spinauris	*peronii* species group

Among the species groups, the *tetradactyla* and the *vivax* groups have morphologically divergent members. Does this divergence question the sister relationship proposed by the MP tree? The *tetradactyla* group has the lowest bootstrap support (9%; Dolman and Hugall 2008: fig. 2), suggesting that additional molecular characters could alter the placement of *C. amax* and *C. tetradactyla*. The bootstrap support (44%) for the *vivax* group is modest, and in spite of divergent SVLs, trunk-scale keeling and other shared morphologies increase the likelihood of sister-group relationships. The three taxa also share a tropical Queensland distribution.

The *fusca* group has the highest diversity with at least 14 species, most (11) occurring in New Guinea and its adjacent islands, although the north Queensland populations likely harbor more species (Donnellan et al., 2009). This group has a broad size range (44–72 mm mean SVL) and diverse coloration, yet the other character states are surprisingly uniform. This morphological uniformity and the high bootstrap support (100%) emphasize the phyletic unity of the group. The uniformity also supports a single ancestor origin for the colonization and subsequent differentiation in New Guinea.

The *peronii* group likely has a single ancestor origin as well. My preceding insular-population analysis suggest the likelihood of greater species diversity in the Moluccas, but it also supports the similarly of the insular populations and the high probability of their membership in a single clade. Morphologically, the *peronii* group seems most similar to the *gracilis* group. The geographic closeness to northwestern Australia offers a likely source for dispersal and colonization by an ancestral member of the *gracilis* group. The origin of *C. nigrauris* remains enigmatic. The coastal habitats of the Greater Sunda Islands have been well surveyed, and no *Carlia* have been discovered. This absence and the greatest morphological divergence of *C. nigrauris* argue for a longer divergence from other group members or a separate origin from a *gracilis* group ancestor. Its survival on a small island is also enigmatic.

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Appendix

1. MATERIALS AND METHODS

This study relies on the character set and definitions used in a review of morphological variation and differentiation of the *Carlia fusca* complex of New Guinea (Zug 2004). The set contains six mensural and 19 scalation characters. Sex and maturity determined by examination of gonads. All statistical analyses used SYSTAT 11 for statistical analysis, and sexual dimorphism between adult females and males relied on Student's t tests and $p \leq 0.05$ differences among pooled variance samples. Characters and their abbreviations are available in Zug (2004).

2. SPECIMENS EXAMINED (HOLOTYPES HIGHLIGHTED IN **BOLD**)

Carlia nigrauris: Java, Pulau Tindjil SMF 53915, 53916, 53917-922, WAM R101496, R101498, R104927.

Carlia peronii: 'Ile de France' MNHN 3037 [locality corrected to Timor by Greer; proposed as vicinity of Kubang, Timor, herein]; Timor, Kokabis WAM R107308, R107312, R107319-320, R107328-340, R107343, R107345, R107355; Samao [= Semau] RMNH 30414, Soë BMNH 1946.8.10.81 [not seen]. Color statistics — Kokabis WAM R107306-307, R107309-311, R107314-318, R107321, R107323-331, R107333-342, R107344, R107346-349, Kupang WAM R107304.

Carlia spinauris:-Timor, Lelogama BMNH 1946.8.16.32, 1946.8.17.58, Djamplong BMNH 1946.8.10.81.

Carlia peronii species group (specific identity not assigned): Flores, Pulau Sukur ZMA 15316A-K; Alor, Apui WAM R107932, R107934, R107937-939, R107941, R107958, R107960, R107965-967, R107974-976, R107978, R107981-982, R107991, R107999; Banda, Bandaneira WAM R109401-402, R109413-414, R109416-417, R109419, R109421-422, R109424-427; Kisar, Nomaha WAM R117421-422, R117424, R117427-430, R117487, Wonreil WAM R117441; Roti, Oeseli WAM R105829, R105836-837, R105839-843; Timor [no additional data] RMNH 7032, 7943, 30412-413; Wetar [no additional data] RMNH 5533, Ilpokil WAM R117509, R117553. Color notes – Semau RMNH 7941; Wetar WAM R117553 (color slide); Kisar WAM R117487 (color slide).

Carlia fusca species group: Timor [no additional data] RMNH 30414, ZMB 4981A-B, ZMDanm [specimens in ZMA collection] 47918-920.

3. MAP RESOURCES FOR FIGURE 1

Southern tier of islands

Java-Tindjil. *Carlia nigrauris:* Mertens 1957a; see preceding Specimens Examined section.

Java-main island. No *Carlia* reported: Barbour 1912; de Rooij 1915; Brongersma 1930, 1931; Mertens 1957a; Crampton et al. 1990; Manthey and Grossmann 1997.

Bali. No *Carlia* species reported: Barbour 1912; Mertens 1930, 1936, 1957b; Brongersma 1931; McKay 2006.

Lombok. No *Carlia* species reported: Barbour 1912; Boulenger 1897; Mertens 1930.

Sumbawa. No *Carlia* species reported: Mertens 1930.

Komodo. No *Carlia* species reported: Dunn 1927; Darevsky 1964; Auffenberg 1980;

Sumba. No *Carlia* species reported: Boulenger 1897; Barbour 1912; Forcart 1949.

Flores. No *Carlia* species reported: Boulenger 1897; Barbour 1912; Mertens 1930.

Pulau Sukur [= Pulau Sukun]. *Lygosoma fuscum*: de Rooij 1915; *Carlia* sp: see preceding Specimens examined.

Solar. No data available.

Alor. *Carlia* sp: see preceding Specimens Examined section.

Roti. *Carlia* sp: see preceding Specimens Examined section.

Wetar. *Carlia* sp: see preceding Specimens Examined section.

Romang. No data available.

Damar. *Lygosoma fuscum*: de Rooij 1915.

Semau. *Carlia peronii*: see preceding Specimens Examined section.

Timor. *Carlia peronii*: Duméril and Bibron 1837, corrected to Timor (Greer, 1976); see preceding Specimens examined. *Carlia spinauris*: Smith 1927; see preceding Specimens Examined section.

Moa. No data available.

Sermata. No data available.

Leti. No data available.

Babar. *Carlia babarensis*: Zug 2004.

Tanimbar. *Carlia babarensis*: Zug 2004.

Northern tier of islands

Sulwawesi. No *Carlia* species reported: Brongersma 1931.

Kepulauan Banggai. No data available.

Ternate. *Lygosoma fuscum*: de Rooij 1915. *Carlia tutela* : Zug 2004. No *Carlia* species reported: Brongersma 1931.

Morotai. *Carlia tutela* : Zug 2004.

Halmahera. *Lygosoma fuscum*: de Rooij 1915. *Carlia tutela* : Zug 2004. No *Carlia* species reported: Brongersma 1931.

Sanana. No *Carlia* species reported: Kopstein, 1926.

Bacan. No data available.

Obi. No data available.

Misool. *Lygosoma fuscum*: de Rooij 1915.

Buru. No *Carlia* species reported: Barbour 1912. *Lygosoma fuscum*: Kopstein, 1926.

Seram. *Leiolopisma fuscum*: Barbour 1912. *Lygosoma fuscum*: de Rooij 1915. *Carlia leucotaenia*: Zug 2004.

Ambon. *Leiolopisma fuscum*: Barbour 1912. *Lygosoma fuscum*: de Rooij 1915. *Carlia leucotaenia*: Zug 2004.

Haruku. *Lygosoma fuscum*: Kopstein 1926.

Saparua. *Lygosoma fuscum*: de Rooij 1915.

Banda Ids. *Lygosoma fuscum*: Kopstein 1926. *Carlia* sp: see preceding Specimens Examined section.

Kepulauan Goram. *Lygosoma fuscum*: de Rooij 1915.

Kai. *Lygosoma beccarii*: Barbour 1912; de Rooij 1915. *Carlia beccarii*: Zug 2004.

4. *CARLIA* SPECIES GROUPS

Morphological and distributional data derive from Ingram and Covacevich (1989) and Zug (2004); the reported states are means for mensural traits and medians for meristic traits.

bicarinata **group**

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate, occasionally tricarinate or mixed (*schmeltzii*); 41–42 and 57 (*schmeltzii*) mm SVL, 42–49% HindlL/SVL, 21–23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 7 (*bicarinata*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, about half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 46–47 Dorsal, 31–35 Midbody, 18–22 3FingLm, 25–29 4ToeLm.

Geography. Subtropical Queensland through Cape York Peninsula, Fly River Plains and Port Moresby area New Guinea.

Sister group. *fusca* group.

Species content. *bicarinata*, *schmeltzii*, *storri*.

fusca **group**

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate; 44–72 mm SVL, 44–56% HindlL/SVL, 21–24% HeadL/SVL; prefrontals seldom in contact, interparietal rarely fused, 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less of lower eyelid area; ear-opening round to oblong vertical with few weakly pointed AuricL on anterior border; 46–50 Dorsal, 31–38 Midbody, 20–24 3FingLm, 26–34 4ToeLm.

Geography. Northern tropical Queensland through Cape York Peninsula, broadly throughout New Guinea and adjacent islands, and eastern Wallacea from Morotai to Kai and Tanimbar islands.

Sister group. *bicarinata* group.

Species content. *fusca*, *longipes*, *mysi*, *quinquecarinata* and others (Table 3).

gracilis **group**

Definition. Dorsal and lateral trunk scales of adults moderately tricarinate; 36–42 mm SVL, 43–46% HindlL/SVL, 21–24% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 or 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD small to modest, usually less half of lower eyelid area; small ear-opening circular to oblong horizontal with 1–2 weakly pointed AuricL on anterior border; 44–46 Dorsal, 28–31 Midbody, 16–17 3FingLm, 21–22 4ToeLm.

Geography. Northern Western Australia and Northern Territory, and southern Cape York Peninsula through northern tropical Queensland.

Sister group. Clade containing all other species groups.

Species content. *gracilis*, *jarnoldae*.

munda **group**

Definition. Dorsal and lateral trunk scales of adults weakly (*munda*) to strongly tricarinate; 40–43 mm SVL, 43–47% HindlL/SVL, 23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 (*munda*)or 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD large, more half of lower eyelid area; ear-opening circular to oblong vertical with 0–2 blunt AuricL on anterior border; 45–47 Dorsal, 30–31 Midbody, 18–20 3FingLm, 23–26 4ToeLm.

Geography. Northwestern Western Australia across northern Australia to subtropical Queensland.

Sister group. *triacantha* group.

Species content. *munda*, *pectoralis*.

peronii group

Definition. Dorsal and lateral trunk scales of adults weakly tricarinate, uncommonly mixed bi- and tricarinate; 37–46 and 57 (*nigrauris*) mm SVL, 40–47% HindlL/SVL, 21–23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening circular with numerous acute lobes around perimeter; 46–53 Dorsal, 32–34 Midbody, 17–21 3FingLm, 23–29 4ToeLm.

Geography. Pulau Tindjil, Java, and Lesser Sunda Islands from Flores through Timor and its adjacent islands.

Sister group. Uncertain.

Species content. *nigrauris, peronii*, *spinauris*.

rhomboidalis group

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate; 41–44 mm SVL, 45% HindlL/SVL, 22% HeadL/SVL; prefrontals seldom in contact, interparietal fused to frontoparietal, 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD small, less than half of lower eyelid area; ear-opening oblong diagonal with 1–2 large AuricL on anterior border; 47 Dorsal, 32–33 Midbody, 19 3FingLm, 27–29 4ToeLm.

Geography. Northern and southern tropical Queensland.

Sister group. Clade containing *tetradactyla* and *vivax* groups

Species content. *rhomboidalis*, *rubrigularis*.

tetradactyla group

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate (*tetradactyla*) or strongly bicarinate (*amax*); 35 (*amax*) and 45 mm SVL, 39 (*tetradactyla*) and 48% HindlL/SVL, 22 (*tetradactyla*) and 25% HeadL/SVL; prefrontals in contact, interparietal separate, 7 (*vivax*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening oblong diagonal or vertical with few blunt AuricL on anterior border; 39 (*amax*) and 50 Dorsal, 31–33 Midbody, 16–18 3FingLm, 22 4ToeLm.

Geography. Northern Western Australia to Northern Territory (*amax*) and subtropical Queensland to eastern Victoria (*tetradactyla*).

Sister group. *vivax* group.

Species content. *amax, tetradactyla*.

triacantha group

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate (*johnstonei*) or tricarinate; 43–45 mm SVL, 39 (*triacantha*) and 42–45% HindlL/SVL, 23% HeadL/SVL; prefrontals usually in contact or rarely so (*johnstonei*), interparietal separate, 7 (*rufilatus*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD small, less than half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 45–50 Dorsal, 29–32 Midbody, 18–19 3FingLm, 22–25 4ToeLm.

Geography. Northern Western Australia and Northern Territory.

Sister group. *munda* group.

Species content. *johnstonei*, *rufilatus*, *triacantha*.

vivax group

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate to weakly tricarinate (*rostralis*); 42–45 (*dogare*, *vivax*) and 59 (*rostralis*) mm SVL, 46–52% HindlL/SVL, 22% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 or 8 (*rostralis*) Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 48–50 Dorsal, 31–35 Midbody, 16 (*vivax*) and 21–22 3FingLm, 24 (*vivax*) and 27–30 4ToeLm.

Geography. Cape York to subtropical Queensland.

Sister group. *tetradactyla* group.

Species content. *dogare*, *rostralis*, *vivax*.

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Neotropical Myrmecophilous Melastomataceae An Annotated List and Key

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An annotated list of and key to all neotropical species of Melastomataceae with ant domatia are presented. Species that have domatia but for which ants have not been reported are also included. Ant domatia or nesting structures are known from 11 genera and 84 species. The great majority of these belong to the genera *Tococa* (30 species), *Clidemia* (27 species) and *Blakea* (9 species). Ants nest in domatia at the apex of the petiole or the blade of the leaf (55 species), the base of the petiole (8 species), hollow stems (16 species), or other open structures such as pseudostipules, open domatia and concave or vaginated petioles (5 species). Myrmecophilous species are distributed throughout the Neotropics from Southern Mexico to Brazil and Bolivia, but they are absent from the Antilles and Trinidad.

KEY WORDS: ant-plants, domatia, Melastomataceae, myrmecophily, Neotropics.

Se presenta una lista anotada y clave para todas las especies neotropicales de la familia Melastomataceae que poseen domacios habitados por hormigas (mirmecodomacios). También se incluyen aquellas especies que tienen domacios pero para las cuales no se han reportado hormigas. En total, mirmecodomacios u otras estructuras habitadas por hormigas están presentes in 11 géneros y 84 especies. La gran mayoría de estas corresponden a los géneros *Tococa* (30 especies), *Clidemia* (27 especies) y *Blakea* (9 especies). Las hormigas habitan domacios en el ápice del pecíolo o la base de la hoja (55 especies), la base del pecíolo (8 especies), tallos huecos (16 especies), u otras estructuras abiertas tales como seudo estipulas o pecíolos cóncavos o invaginados (5 especies). Melastomataceae con mirmecodomacios se encuentran distribuidas en todo el Neotrópico desde el sur de México hasta Bolivia y Brasil, pero están ausentes en las Antillas y Trinidad.

Myrmecophites, or plants that house ants, are found throughout the tropics in wet and seasonal environments. In the New World these associations are known to occur in over 60 genera from 22 plant families (Benson 1985; Jolivet 1996). In the Neotropics, mymecophytes are particularly diverse among the Melastomataceae, where species from 10 genera have been reported to house ants. Even though many of the myrmecophitic Melastomataceae have been treated in regional floras or in taxonomic revisions for individual genera, no comprehensive list for all myrmecophites has ever been published. Because of their conspicuous domatia, and the fact that many of them are locally abundant forest understory shrubs (thus easily seen and collected by field biologists), there are usually large amounts of undetermined specimens at every herbarium with a strong neotropical collection. However, it is often the case that many mymecophytic species grow in the same area, which leads to many specimens being misidentified as the most common species or genus occurring in a given area. For example, most myrmecophites in Central America are in the genus *Clidemia*, so specimens of *Tococa*, *Henriettea*, *Maieta* and *Conostegia* are filed as *Clidemia* sp. in many local herbaria. These same reasons have led to a large number of species descriptions, with often the same taxon being placed in two or three different genera.

Additionally, the lack of a comprehensive list has also led to different names being applied to the same taxon depending of the provenance of the specimen. This has resulted in an ever increasing number of synonyms (see text and Appendix). Moreover, of the 10 genera of Melastomataceae with myrmecophites, only *Allomaieta* (Lozano and Becerra-de-Lozano 1999), *Conostegia* (Schnell 1996), *Maieta* (Whiffin 1971) and *Tococa* (Michelangeli 2005) have been revised or monographed in the last 30 years. Therefore, for the other six genera, we do not even have a clear understanding of total number of species and which ones are myrmecophites. This is especially true for *Clidemia*, which was last monographed by Cogniaux (Cogniaux 1891), and for which there are as many as 30 species names applied to myrmecophites.

The present study is intended as a comprehensive list and key of myrmecophitic Melastomataceae, accompanied by diagnostic characters for each species, and a brief review of the domatia types present in the family and the ecology of ant-plant interactions.

ANT DOMATIA.— In myrmecophitic Melastomataceae, ants inhabit a variety of structures in different organs of the plant. Most of these can be considered domatia in the strict sense, whereas others are less specialized structures commonly found in other species of Melastomataceae but that occasionally are used as nesting structures (e.g., floral bracts, grooved petioles, etc.).

Specialized ant domatia can be either primary (stem derived) or secondary (leaf derived) (Benson 1985; Jolivet 1996). Four species of *Miconia*, three species of *Topobea*, six species of *Blakea*, two species of *Conostegia*, and one of *Merianthera* have hollow stem domatia (primary domatia *sensu* Benson). Domatia at the base of the petiole are restricted to eight species of *Clidemia*, whereas ant domatia at the apex of the petiole or the base of the blade are present in 55 species.

Some species of *Clidemia* with either leaf blade (e.g., *C. rodriguezii*) or petiole-base domatia (e.g., *C. ciliata*) have large domatia that certainly resemble those of myrmecophitic species, but field and herbarium studies have failed to reveal the presence of ants. Other species like *Blakea chlorantha* and *B. austin-smthii* have large domatia that do not house ants, but that given their morphology can sometimes be referred to as myrmecophites. These and other species for which myrmecophitism has not yet been confrirmed are also included in this list because they might later be found, indeed, to be myrmecophites and/or because researchers might try to determine them using this key given their resemblance to known myrmecophites. In any event, the appropriate discussion follows the pertinent species entries.

THE ROLE OF THE ANTS.— Not only do ants nest in a variety of structures, but the role of the inhabiting ants seems to vary across ant species and/or plant species. Several studies have shown that inhabiting ants protect the plants from potential herbivores (Vasconcelos 1991; Vasconcelos 1993; Tennant 1994; Forero and Ahumada 1997; Bizerril and Vieira 2002; Michelangeli 2003). Moreover, the degree of protection conferred by the ants can vary either across environments or across ant species (Michelangeli 2003; Bruna et al. 2004). Additionally, some ants may play a role in plant-plant competition for light and nutrients. *Myrmelachista* ants prune the vegetation surrounding their host (usually *Tococa guianensis* or *Clidemia heterophylla*), resulting in monospecific stands in the forest understories known as "supay chacras" or devil gardens (Svoma and Morawetz 1992; Renner and Ricklefs 1998). Lastly, some species of myrmecophitic melastomes use the ant waste products as a source of nutrients, particularly nitrogen (Cabrera and Jaffe 1994; Solano and Dejean 2004), not unlike what has been found for several old world myrmecophites like *Myrmecodia* (Huxley 1978) or *Dischidia* (Treseder et al. 1995).

KEYS

The following key is not natural given that myrmecophitic Melastomataceae form a polyphyletic assemblage. Inasmuch as possible, vegetative characters (particularly derived from domatia), were used in building this key. Portions of this key have been modified from regional floristic and taxonomic treatments (Gleason 1931; Wurdack 1973, 1980; Wurdack et al. 1993; Schnell 1996; Almeda 2001; Michelangeli 2005). Because generic delimitations are mostly based on floral characters, species from the same genus often key out in different sections of the key. Two undescribed species are also included because material has already been distributed to several herbaria. Some species have large domatia-like structures, but no ants have been reported either in field studies or found in herbarium specimens. These species are included in the key as well as in the list that follows along with the appropriate annotations.

Some species in the Miconieae, most commonly in the genus *Clidemia*, have pseudolateral inflorescences. These are inflorescences that are terminal early in development but become lateral by overtopping of the axillary meristem (Judd 1986, 1987). Most of these species are included in this key only under the axillary inflorescence group because they become pseudolateral so early in development that they are seldom found in this state. However, some species have pseudolateral inflorescences that appear lateral only at or near anthesis of the flowers, so they look terminal for longer period of times. These species can be keyed out under either couplet of the key.

Main Key

1. Structural domatia absent, ants nesting in open structures such as modified bracts, pseudo-stipules or vaginated petioles. . . . . **Subkey 1**

1'. Structural domatia present, domatia formed by hollow stems or paired ascidia at the base or apex of the petioles or the base of the leaf.

    2. Domatia present as hollow stems (primary domatia) . . . . **Subkey 2**

    2'. Domatia as paired ascidia at the base or apex of the petioles or the base of the leaf.

        3. Domatia at the base of the petiole, often appearing adnate to the stem. . . . . . **Subkey 3**

        3'. Domatia at the apex of the petiole, or the base of the leaf blade . . . . **Subkey 4**

Subkey 1: Structural domatia absent, ants nesting in open structures such as modified bracts, pseudo-stipule or vaginated petioles

1. Ants nesting in inflorescence bracts . . . . *Blakea polyantha*

1'. Ants nesting in vaginated petioles or pseudo-stipules developing at the nodes.

    2. Ants nesting at the base of vaginated petioles; flowers not subtended by two pairs of imbricate bracts; shrubs . . . . *Clidemia ferox*

    2'. Ants nesting in pseudo-stipules up to 6 cm long developing at the nodes; flowers subtended by two pairs of imbricate bracts; trees or hemiepiphytes. . . . . *Blakea jativae*

Subkey 2: Domatia present as hollow stems (primary domatia)

1. Inflorescences terminal, flowers not subtended by a pair of imbricate bracts.

    2. Ovary superior, fruits capsular; petals magenta . . . . *Merianthera burlemarxii*

    2'. Ovary at least partly inferior, fruits berries; petals white, grennish or light pink.

        3. Calyx calyptrate, circumcise; flowers pleiostemonous.

            4. Hypanthium tetragonal and winged, petals 4 . . . . *Conostegia inusitata*

            4'. Hypanthium terete and lacking wings, petals (6–) 7–12 . . . . *Conostegia* sp. A

3'. Calyx persistent; flowers diplostemonous or pleiostemonous.
5. Stems terete to quadrate . . . . *Miconia hospitalis*
5'. Stems obviously quadrangular.
6. Hypanthium conspicuously winged (in buds wings only noticeable at the base of the hypanthium), flowers 4–5-merous . . . . *Miconia bailloniana*
6'. Hypanthium terete to slightly 10-costate, flowers 5-merous.
7. Leaves 5-plinerved; flowers diplostemonous. . . . . *Miconia expansa*
7'. Leaves 3-plinerved; flowers diplostemonous or pleiostemonous . . . . *Miconia flaccida*
1'. Inflorescences lateral, flowers subtended by a pair of imbricate bracts.
8. Leaf petioles terete.
9. Anthers oblong to ovate, the apex round to obtuse, opening by two (usually small) separate apical pores.
10. Internodes 1–4 cm long, stem domatia ovoid to quadrangular; leaves shortly plinerved . . . . *Blakea perforata*
10'. Internodes 4–12 cm. stem domatia fusiform; leaves basally nerved . . . . *Blakea podagrica*
9'. Anthers linear-oblong to subulate, the apex truncate to acute, opening by two confluent dorsal pores.
11. Leaves 5–7-plinerved, with mite domatia on the abaxial surface formed by tufts of hairs a the union of the primary vein and the first pair of secondary veins . . . . *Topobea pluvialis*
11'. Leaves 3–5-nerved, without abaxial mite domatia.
12. leaves 5-nerved, calyx lobes inconspicuous to irregular. . . . *Topobea gracilis*
12'. leaves 3-nerved, calyx lobes apiculate. . . . . *Topobea inflata*
8'. Leaf petioles vaginate to decurrent.
13. Leaves plinerved, the base obviously decurrent, so the entire petiole is vaginate . . . . *Blakea involvens*
13'. Leaves basally nerved, the base not decurrent, petiole vaginate only towards the base.
14. Anther connective with a developed dorso-basal appendage, stigma punctate to slightly expanded . . . . *Blakea subvaginata*
14'. Anther connective base simple, lacking appendages; stigma capitate.
15. Style glabrous . . . . *Blakea punctulata*
15'. Style pubescent. . . . . *Blakea subconnata*

Subkey 3: Domatia as paired ascidia at the petiole bases, often appearing adnate to the stem

1. Inflorescences over 12 cm long.
2. Flowers 5-merous . . . . *Clidemia neblinae*
2'. Flowers 4-merous . . . . *Clidemia* sp. A
1'. Inflorescences less than 10 cm long.
3. Petioles less than 40 mm long, leaf base cordate.
4. Domatia developed unilaterally at the base of the petiole . . . . *Clidemia pilosa*
4'. Domatia developed on both sides of the petiole.
5. Leaf abaxial pubescence of stellate hairs . . . . *Clidemia ciliata* var. *elata*
5'. Leaf abaxial pubescence of simple setae . . . . *Clidemia ciliata* var. *testiculata*
3. Petioles > 60 mm long, leaf base acute to cordate.

6. Stem pubescence with glandular and non-glandular setae over 4 mm long, barbellate hairs 0.5 mm long present . . . . *Clidemia allardii*

6'. Stem pubescence with glandular and non-glandular setae less than 4 mm long (rarely up to 5 mm long), barbellate hairs absent.

7. Lower half of the hypanthium glabrous to very sparsely pubescent . . . . *Clidemia tococoidea*

7'. Lower half of the hypanthium setose . . . . *Clidemia crenulata*

Subkey 4: Domatia as paired ascidia at the apex of the petiole or the base of the leaf blade

1. Domatia at the base of the leaf blade, formed by saccate ascidia with the basal and lateral margins decurrent, but free from the petiole, not opening to the exterior through holes on the adaxial surface of the leaf at the union of the midvein and first pair of diverging primary veins.

2. Pubescence of uppermost internodes consisting of hairs 1–2 mm long; leaf blades denticulate and revolute on drying; outer floral bracts linear-lanceolate, 15–21 mm long, equaling or exceeding the calyx lobes at anthesis. . . . . *Blakea austinsmithii*

2'. Pubescence of uppermost internodes consisting of hairs mostly less than 0.5 mm long; leaf blades entire; outer floral bracts ovate to elliptic-ovate, 5.5–9 mm long, conspicuously shorter than the calyx lobes at anthesis . . . . *Blakea chlorantha*

1'. Domatia at the apex of the petiole, or if at the base of the blade, then not decurrent and free from the petiole, only opening to the exterior through small holes on the abaxial surface at the point of union of the midvein and the first pair of primary veins.

3. Flowers subtended by two pairs of imbricate bracts, 6-merous; leaves with non obvious tertiary venation, the majority of secondary veins thin and straight . . . . *Blakea formicaria*

3'. Flowers not subtended by two pairs of imbricate bracts, 4–7-merous; leaves with obvious tertiary venation, secondary veins often branched or angling.

4. Leaves strongly anisophyllous, the smaller one always lacking domatia.

5. Inflorescences terminal, racemes or panicles 9–30 cm long.

6. Inflorescence an unbranched raceme; flowers sessile 5-merous; outer calyx acute, ... *Tococa racemifera*

6'. Inflorescence a branched panicle; flowers pedicellate, 6-merous; outer calyx filiform, 11–16 mm long. . . . . *Tococa filiformis*

5' Inflorescences lateral, cymes or panicles up to 13 cm long.

7. Flowers haplostemonous, fruit a dehiscent capsule . . . *Allomaieta grandiflora*

7'. Flowers diplostemonous, fruit a berry.

8. Flowers 6-merous; outer calyx laterally connate, forming a "skirt" 1.5–2.5 mm wide around the hypanthium . . . . *Tococa macrosperma*

8'. Flowers 4–5-merous; outer calyx reduced or adnate to the inner calyx, but never connate.

9. Domatia abaxial surface even with the remainder of the leaf blade; bracts ovate to lanceolate; anthers incurved, thecae surface rugose; stigma capitate.

10. Hypanthium 10-winged, glandular setose on the wings, but otherwise glabrous. . . . . *Maieta neblinensis*

10'. Hypanthium terete, the surface sparsely to moderately stellate, often glandular setose.

11. Flowers in short cymes; bracteoles one pair, 1.3–1.6 mm long. . . . . *Maieta poeppigii*

11'. Flowers solitary; bracteoles two or three pairs, 4–7.5 mm long, the outermost pair united at the base . . . . *Maieta guianensis*

9'. Domatia abaxial surface protruding from the leaf blade; bracts setaceous or inconpicuous; anthers straight, thecae surface smooth; stigma truncate to funnelform.

12. Domatia bearing along the medial dorsal line 2–9 leaf-like appendages 2–6.5 mm long . . . . *Clidemia foliosa*

12'. Domatia lacking any leaf-like appendages.

13. Petiole below the domatium > 4 cm long; petal apex acute . . . . *Ossaea bullifera*

13'. Petiole below the domatium < 2 cm long; petal apex round to emarginate.

14. Flowers (6–)7-merous; domatia 1.2–3(–4.5) cm long, elongate . . . . *Clidemia heptamera* p.p

14'. Flowers 4–5-merous; domatia 0.8–1.5 cm long, ovoid

15. Flowers 4-merous . . . . *Clidemia sprucei*

15'. Flowers 5-merous.

16. Inflorescences sessile or with the peduncule < 1 cm long; hypanthium stellate puberulous . . . . *Clidemia inobsepta*

16'. Inflorescence peduncule > 2 cm long; hypanthium densely setose . . . . *Clidemia heterophylla*

4'. Leaves isophyllous, or if anisophyllous, at least some of the smaller leaves bearing domatia.

17. Domatia surface with numerous orifices, verrucose and glabrous.

18. Inflorescence a condensed raceme; petals green . . . . *Tococa spadiciflora*

18'. Inflorescence a branched panicle; petals white to pale pink . . . . *Clidemia killipii*

17'. Domatia surface without orifices, generally smooth, or if verrucose, then pubescent.

19. Inflorescences caulinar . . . . *Henriettea cuneata*

19'. Inflorescences lateral or terminal.

20. Calyx calyptrate, circumcissilly dehiscent at anthesis, flowers pleiostemonous

21. Calyx dehiscing irregularly above the torus; stamens 13–14 . . . . *Tococa carolensis*

21'. Calyx dehiscing regularly at the torus; stamens >15.

22. Domatia at the base of the leaf blade, extending into the apical portion of the petiole, leaf base decurrent; petals 9–10 mm long; stamens 15–17, anthers recurved at the base . . . . *Conostegia dentata*

22'. Domatia at the base of the leaf blade, not extending into the petiole; petals 6–7 mm long; stamens 18–29, anthers straight to sinuate . . . . *Conostegia setosa*

20'. Calyx truncate and/or persistent, not circumcissilly dehiscent at anthesis, flowers diplostemonous.

23. Anthers connivent, with a triangular dorsal connective appendage projecting downward from the union between the anther and the filament . . . . *Tococa symphyandra*
23'. Anthers free, without appendages, or if the appendages present these not dorsal triangular projecting downward from the union between the anther and the filament.
24. Inflorescences, at least during development, subtended by large bracts, at least 2 × 2 cm.
25. Domatia immersed in the leaf blade . . *Tococa cordata* p.p.
25'. Domatia free from the leaf blade.
26. Bracts early caducous, > 5 cm long; the stem with non-glandular stiff trichomes 12–15 mm long . . . . *Tococa leticiana*
26'. Bracts persistent through anthesis, < 3.5 cm long; the stem glabrous to glandular puberulous, the trichomes less than 9 mm long . . . . *Tococa costoides*
24. Inflorescences ebracteate, or with bracts < 5 mm wide 27
27. Hypanthium winged or ridged, or if terete, then with the calyx or a discrete line of trichomes extending downwards, opposite the calyx lobes.
28. Domatia completely embedded in the leaf blade, often occupying up to ⅕ of the leaf surface. . . . . *Tococa rotundifolia*
28'. Domatia free from the leaf surface.
29. Hypanthium with twice as many ribs as petals, one set alternating with the calyx, the other opposite the calyx.
30. Hypanthium wings thin, projecting less than 1.5 mm from the surface of the hypanthium.
31. Hypanthium and leaf pubescence with a mix of glandular and simple setae; leaves oblong to ovate . . . . *Tococa stephanotricha*
31'. Hypanthium and leaf pubescence with simple setae; leaves lanceolate to oblong lanceolate . . . . *Tococa stellata*
30'. Hypanthium wings broad, projecting over 2–4 mm from the surface of the hypanthium.
32. Flowers 5-merous . . . . *Tococa gonoptera*
32' Flowers 4-merous . . . . *Tococa quadrialata*
29'. Hypanthium with as many ribs as petals, opposite the calyx.
33. Leaves broadly lanceolate . . . . *Tococa pauciflora*
33'. Leaves elliptic to obovate.
34. Inflorescence axis square and clearly winged; calyx projecting above the torus. . . . . *Tococa stenoptera*
34'. Inflorescence axis terete flattened, wings absent; calyx not projecting above the torus . . . . *Tococa macroptera*
27'. Hypanthium terete, never with the calyx or a discrete line of trichomes extending downwards opposite the calyx lobes or without ridges or wings opposite the calyx.
35. Inflorescence axillary or pseudoaxillary (initially terminal, but becoming lateral by growth of the terminal meristem).
36. Young stems quadrate and winged, domatia < 1 cm long . . . . . . *Clidemia rodriguezii*
36'. Young stems terete to flattened, domatia > 1 cm long.

37. Domatia completely to ⅘ immersed in the leaf blade.
38. Leaf surface bullate . . . . *Clidemia spectabilis*
38'. Leaf surface smooth.
39. Leaves 7–9-plinerved, the domatia fusiform, restricted to the adaxial surface and completely immersed in the leaf blade . . . . *Clidemia lanuginosa* p.p.
39'. Leaves 5–7-nerved, or if plinerved then the domatia ovoid, visible on both surfaces of the leaf, and often slightly projected into the apex of the petiole.
40. Leaf abaxial surface glabrous (but pubescent on the primary and secondary veins); stem sparsely pubescent, the trichomes up to 11 mm long . . . . *Clidemia pubescens* p.p.
40'. Leaf abaxial surface sparsely to densely pubescent, the trichomes 3–14 mm long; stem densely pubescent, the trichomes 10–16 mm long. . . . . *Clidemia acostae*
37'. Domatia free from the leaf blade or extending into the leaf blade up to 2/3.
41. Flowers (6–) 7-merous . . . . *Clidemia heptamera* p.p.
41'. Flowers 4–5-merous.
42. Domatia fusiform to oblong, the apex immersed in the leaf blade.
43. Petiole (including the domatia) > 6 cm long; leaf base cordate, 8–17 cm wide; inflorescences > 6 cm long . . . . *Clidemia folsomii*
43'. Petiole (including the domatia) < 4.5 cm long; leaf base obtuse to acute, or if cordate, then < 6 cm wide; inflorescence < 5 cm long.
44. Leaves 5-plinerved or 5–7-nerved.
45. Leaves 5-plinerved; torus inner surface with a ring of short glandular trichomes . . . . *Clidemia ayangannensis*
45'. Leaves 5–7-nerved; torus inner surface without a ring of short glandular trichomes. . . . . *Clidemia myrmecina*
44'. Leaves 7–9(–11)-plinerved.
46. Leaves > 22 cm long, elliptic; inflorescences axillary and paired at the nodes; anther thecae white . . . . *Clidemia tenebrosa*
46'. Leaves < 20 cm long, ovate (rarely ovate-elliptic); inflorescences pseudo-axillary, not paired at the nodes; anther thecae yellow . . . . *Clidemia collina*
42'. Domatia ovoid to ovate, completely free from the leaf blade.
47. Domatia with an apical ascending lobe on each side . . . . *Tococa macrophysca*
47'. Domatia without an apical ascending lobe on each side.
48. Leaves obovate, the base acute . . . . *Clidemia juruensis*
48'. Leaves ovate to ovoid, the base cordate to obtuse.
49. Inflorescence peduncle > 2.5 cm long; leaves ovate to oblong-ovate; flowers 4–5-merous.
50. Leaves plinerved (rarely basally nerved); inflorescence erect, petals pink to light red . . *Clidemia pubescens* p.p.
50'. Leaves basally nerved; inflorescence pedular or perpendicular to the stem, petals white to light pink . . . . . .

. . . . *Clidemia setosa*

49'. Inflorescence peduncle > 2.5 cm long; leaves elliptic to ovate elliptic; flowers 5-merous.

51. Leaf adaxial surface glabrous, domatia pubescence > 7 mm long; stem pubescence adpressed. . . . . *Clidemia ventricosa*

51'. Leaf adaxial surface pubescent, domatia pubescence < 5 mm long; stem pubescence retrorse or spreading . . . . *Clidemia taurina*

35'. Inflorescence terminal, even late in development.

52. Domatia immersed in the base of the leaf blade or the constriction between the domatium and the blade more than ⅔ the width of the domatia.

53. Leaves 7–9-plinerved . . . . *Clidemia lanuginosa* p.p.

53'. Leaves basally nerved or 3–5-plinerved.

54. Domatia, in at least some leaves, occupying more than ⅕ of the total length of the leaf. . . . . *Tococa ciliata*

54'. Domatia in all the leaves occupying less than ⅕ of the length of the leaf.

55. Anthers yellow or cream; fruits black at maturity; seeds glabrous.

56. Leaf blade surface foveolate; thecae > 6 mm long . . . . *Tococa obovata* subsp. *neblinensis*

56'. Leaf blade surface flat; thecae < 4.5 mm long.

57. Inflorescence a short panicle subtended by an early caducous bract 2–3 cm long, flowers on pedicels 6–11 mm long; petals white; anther connective with a small dorso-basal tooth; ovary 3–celled. . . . . *Tococa hirta*

57'. Inflorescence a raceme, with the central pedicel thickened, flowers sessile; petals orange to brownish; anther connective without a dorso-basal tooth; ovary 4-celled. . . . . *Tococa pachystachya*

55'. Anthers blue or purple; fruits blue at maturity; seeds covered with glandular trichomes.

58. Leaves lanceolate, the domatia ½ or more of the total width of the leaf . . . . *Tococa lancifolia*

58'. Leaves elliptic to ovate, the domatia less than ¼ the width of the leaf.

59. Inflorescence capitate; flowers sessile . . . . *Tococa capitata*

59'. Inflorescence a terminal lax panicle.

60. Calyx outer teeth minute, inner teeth flat and membranaceous . . . . *Tococa cordata* p.p.

60'. Calyx outer teeth subulate, calyx outer teeth truncate or reduced.

61. Hypanthium > 5.5 mm long; ovary ½ superior. . . . . *Tococa coronata*

61'. Hypanthium < 4.5 mm long; ovary completely inferior . . . . *Tococa caudata*

52'. Domatia at the apex of the petiole, free from the leaf blade, the constriction between the domatium and the blade less than ½ the with of the domatia.

62. Anthers with an orbicular gland on the dorsal side of the connective.
    63. Flowers 4-merous; hypanthium glabrous . . . . *Tococa parviflora*
    63'. Flowers 5-merous; hypanthium with stellate hairs . . . . . . *Tococa caquetana*
62'. Anthers without an orbicular gland on the dorsal side of the connective.
    64. Outer teeth of the calyx not or barely projecting (< 0.5 mm) above the inner teeth.
        65. Inflorescence a condensed head . . . . *Tococa undabunda*
        65'. Inflorescence a panicle.
            66. Inflorescence a multiple branched panicle, at least at the base. . . . . *Tococa guianensis*
            66'. Inflorescence a single branched panicle throughout . . . . *Tococa bullifera*
    64'. Outer teeth of the calyx projecting above the inner teeth 0.5–10.0 mm.
        67. Flowers 6-merous; calyx outer teeth projecting >6 mm above the torus . . . . *Tococa filiformis*
        67'. Flowers 5-merous; calyx outer teeth projecting <5 mm above the torus
            68. Domatia elliptic to narrowly ovate; inflorescence obviously terminal; petals light yellow . . . . *Tococa aristata*
            68'. Domatia with an apical ascending lobe on each side; inflorescence terminal, but becoming lateral by overtopping of the axillary meristem; petals white to light pink . . . . *Tococa macrophysca*

ANNOTATED LIST

Some species are polymorphic for the presence of domatia, and they have been noted in the individual species entries with an * preceding the taxon name. For some of these polymorphic species, different infraspecific taxa have been described; if the typical subspecies or variety does not have domatia, the taxon is preceded by **, and the myrmeophytic infraspecific taxon included below. An alphabetical list of homotypic and heterotypic synonyms is provided in the Appendix.

ALLOMAIETA: 8 species, 1 myrmecophite. The genus *Allomaieta* is vegetatively similar to *Maieta*, with strongly anysophyllous leaves and domatia inmmersed in the base of the leaf blade. *Allomaieta grandiflora* is, however, the only myrmecophite in the family with capsular fruits. Calyptrate flowers are also present in *Conostegia* and some *Miconia*, but the latter has baccate fruits, pleiostemonous flowers (haplostemonous in *Allomaieta*), and its myrmecophitic species are isophyllous. *Allomaieta* was recently revised by Lozano and Becerra-de-Lozano (1999).

*__Allomaieta grandiflora__ Gleason, Bull. Torrey Bot. Club, 56(2):98. 1929. TYPE: COLOMBIA. Cundinamarca: Paime. *Bro. A. Joseph 1083* (holotype: US; isotypes: F, GH, NY).

Shrub; leaves dimorphic, the larger one with the domatia immersed in the leaf blade; calyx calyptrate, flowers haplostemonous; ovary inferior, fruits capsular.

Endemic to Colombia, 1000–1550 m.

Not all specimens of *A. grandiflora* have domatia. However, because this species is known from only a handful of specimens, it is hard to determine if this is due to actual polymorphism among individuals, or if in the same individual some branches might bear domatia, while others do not.

Blakea: ca. 150 species, 9 myrmecophites. *Blakea* is a genus of small trees, climbers and epiphytes that together with *Topobea*, *Chalybea*, and *Huilaea* they form the tribe Blakeeae, with the generic limits between *Blakea* and *Topobea* not clearly established (Penneys et al. 2004a). *Blakea* presents a high diversity of domatia types (hollow stems, ascidia at the apex of the petiole and leaf blade tissue extending over the adaxial surface of the petiole) and ants nesting on other structures (floral bracts, vaginated petioles and pseudostipules). Some species have swollen stem nodes, but no specimen has been found with the characteristic holes bored by the ants (i.e., *B. glabrescens*, *B. repens*, etc.), so these species are not included in the key.

Blakea austin-smithii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., 18(4):1561. 1938. Type: COSTA RICA. Alajuela: Palmira, 2200 m, Mar 1938, *Austin Smith H382* (holotype: F; isotype: MO).

Hemiepiphyte; domatia at the base of the leaf blade, prolonged adaxially over the apex of the petiole, but not fused to the petiole; flowers 6-merous, subtended by two pairs of imbricate bracts; outer bracts 15–21 mm long, exceeding the calyx lobes at anthesis. Fig. 1A.

Costa Rica, cloud forests 1500–2400 m.

No ants have been found in the domatia of this species, but some specimens have been annotated as having ant-domatia. *Blakea austin-smithii* and *B. chlorantha* are included in this key because the size of their domatia might prompt collectors to think they are in the presence of a myrmecophite.

Blakea chlorantha Almeda, Rhodora, 82 (832):609, f. 1. 1980. Type: COSTA RICA. Puntarenas: 3–3.5 km SE of Santa Elena and 2–3 km E of Monteverde on the Peñas Blancas trail, Cordillera de Tilarán, 1500–1540 m, 19 Dec 1973, *F. Almeda et al. 2005* (holotype: DUKE; isotypes: CAS, CR, MO, NY, US).

Hemiepiphyte; domatia at the base of the leaf blade, prolonged adaxially over the apex of the petiole, but not fused to the petiole; flowers 6-merous, subtended by two pairs of imbricate bracts; outer bracts 5.5–9 mm long, not exceeding the calyx lobes at anthesis.

Costa Rica, cloud forests 1000–1800 m.

As in the case of *B. austin-smithii*, no ants have been found in the domatia of this species.

Blakea formicaria Wurdack, Mem. New York Bot. Gard., 16:43, f. 5a–e. 1967. Type: ECUADOR. Morona-Santiago/Zamora-Chinchipe: Cordillera Cutucú, *W.H. Camp E-1137* (holotype: US; isotype: NY).

Climbing shrub or epiphytic vine; leaves isomorphic, domatia completely inmersed in the leaf blade, up to 15 mm long; flowers 6-merous, petals white.

Ecuador in montane forests 1000–1700 m.

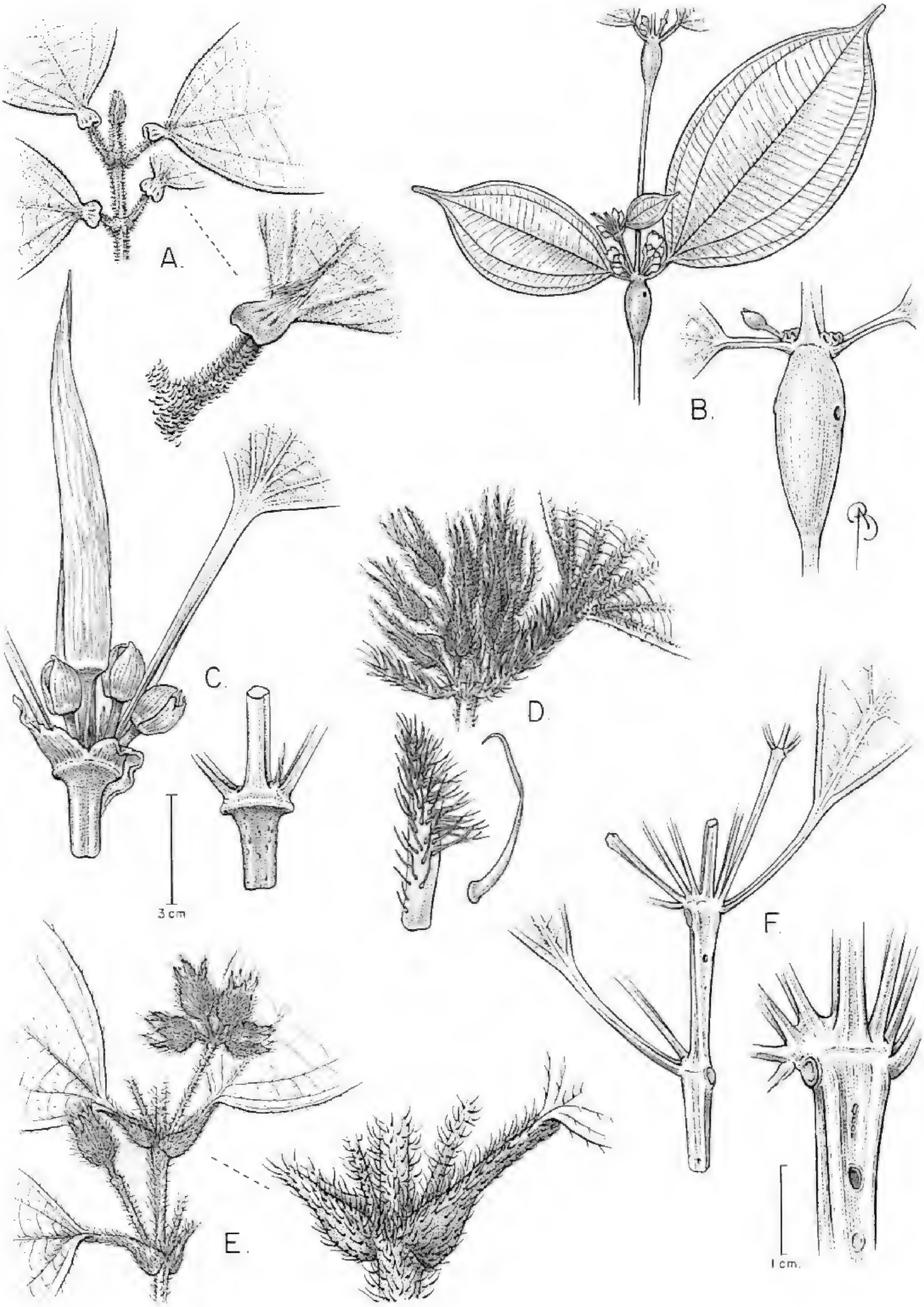
Blakea formicaria is the only species in the Blakeeae with truly petiolar domatia. All other myrmecophitic species in the tribe have either swollen hollow stems or ants nesting in pseudostipules and bracts.

***Blakea involvens** Markgraf, Notizbl. Bot. Gard. Berlin-Dahlem, 14:33. 1938. Type: ECUADOR. Pichincha: 150 m, *Schultze-Rhonhof 1947* (holotype: B[destroyed]).

Hemiepiphyte; primary domatia in hollow swollen twigs (not all specimens); leaves 5-plinerved, the base decurrent on the vaginated petioles; flowers 6-merous, stigma capitate.

Ecuador, 150–1500 m.

Blakea involvens belongs to a group of species with vaginated petioles, some of which have swollen hollow stems (*B. punctulata*, *B. subconnata* and *B. subvaginata*) or swollen stems without


A.
B.
C.
D.
E.
F.
3 cm
1 cm.

domatia (*B. glabrescens*, B. *platypoda*, *B. schultzei*, among others). This group is extremely complex, with several intermediates between species and is in need of a careful revision (D. Penneys, per. comm.)

Blakea jativae Wurdack, Phytologia 43:343. 1979. TYPE: ECUADOR. Esmeraldas: junction of Río San Juan and Río Camumbi near Tobar Donoso, 150 m, 25 Jul 1966, *C. Játiva* & *C. Epling 1128* (holotype: US; isotypes: NY, US).

Hemiepiphyte; young nodes with stipule like structures, 3.5–6 × 1–1.5 cm, membranaceous and hyaline; leaves 7(–9)-nerved, 12–36 cm long; flowers 6-merous, petals white at the base, purple distally, anthers grouped to one side giving a zygomorphic appearance. Fig. 1C.

Ecuador, 250–2200 m.

Ants occasionally nest in between the psedustipules. *Blakea jativae* belongs to a group of species with pseudostipules that includes *B. eriocalyx* and *B. lanuginosa*, but these species have smaller pseudostipules (up to 2 cm long) and no ants have been reported to nest in these structures.

Blakea perforata Almeda, Novon, 10:311. 2000. TYPE: PANAMÁ. Panamá: area surrounding Rancho Chorro, Cañazas mountains abouve Tortí Arriba, 400–700 m, 3 Dec 1977, *J. Folsom et al. 6740* (holotype: CAS; isotype: MO).

Epiphytic or hemiepiphytic shrub; stems quadrate with swollen nodes, often with a hole 1–2 mm diam. that leads to a hollow chamber, internodes 1–4 cm long; leaves 3 (–5) shortly plinerved; inflorescence lateral; outer floral bracts up to 2.5 cm long, acuminate, fused at the base, with 3–5 obvious nerves; flowers 6-merous.

Panamá, 400–700 m.

Blakea podagrica Triana, Trans. Linnean Soc. London, 28:149. 1871. SYNTYPES: COLOMBIA: Barbacoas, 300 m, *Triana 4091*, *4092* (syntypes COL; isosyntypes NY). [According to L. Uribe (1976), *Triana 4092* should be considered the type because the label information matches the protolog].

Blakea podagrica subsp. *ciliata* Wurdack, Phytologia, 6:3. 1957. TYPE: COLOMBIA. Valle del Cauca: Mar 1947, *J. Cuatrecasas 23976* (holotype: F; isotype: NY).

Epiphytic or hemiepiphytic shrub; stems terete, swollen below the nodes, often with a hole 1–2 mm diam. that leads to a hollow chamber, internodes 4–12 cm long; leaves 3–5 nervate; inflorescence lateral; outer floral bracts up to 2.8 cm long, acuminate, fused at the base, with 3–5 obvious nerves; flowers 6-merous.

Colombia, 100–1500 m.

Blakea polyantha Wurdack, Phytologia, 48:250. 1981. TYPE: ECUADOR: Carchi: wet montane forest near El Pailon, ca. 45 km below Maldonado on a path to Tobar Donose, 800 m, 2 Dec 1979, *M. T. Madisson & L. Besse 7269* (holotype: US; isotype: SEL).

Trees up to 7 m tall; stems and petioles with dense thick trichomes up to 11 mm long; nodes with pseudostipules up to 4 cm long, caducous; leaves 30–40 cm long, (7–)9-nerved; inflorescences lateral, flowers 6-merous, subtended by two pair of bracts, free, 17–23 mm long, lanceolate acuminate, densely pubescent towards the apex, less so at the base, the trichomes 2–5 mm long. Fig. 1D.

FIGURE 1. Different domatia and ant nesting structures in Neotropical Melastomataceae. A. *Blakea austinsmithii* with domatia (possibly for mites) on the adaxial surface of the leaf and projecting over the petiole; B. *Topobea inflata* with swollen hollow nodes; C. *Blakea jativae* with pseudostipules; D. *Blakea polyantha* with large floral bracts; E. *Clidemia ferox* with concave petiole base; F. *Miconia bailloniana* with hollow stems. Scale bar = 3 cm for general views, and = 1 cm in details to the right of general view. (A from *Lumer 1302*, B from *Cuatrecasas 16915*, C from *Beck 3082*, D from *Cotton 1812*, E from *Prance 20624*, F from *Schunke-Vigo 11796*; all specimens at NY).

Ecuador, 600–1000 m.

Many specimens of *B. polyantha* have ants nesting build among the trichomes of the bracts, and occasionally the young stems.

***Blakea punctulata** (Triana) Wurdack, Phytologia, 43:354. 1979. *Topobea punctulata* Triana, Trans. Linn. Soc. Bot. 28:150. 1871. TYPE: COLOMBIA: 1851–1857, *Triana s.n.* (holotype: P).

Hemiepiphyte; young stems flattened to terete, internodes 4–10(–30) cm long, often apically swollen and with domatia; leaves 5-nerved, 9–14 cm long, petioles vaginated; flowers 6-merous, anthers with a dorsal connective appendage; style glaborus, stigma capitate.

Colombia, Ecuador, 500–2000 m.

Blakea subconnata Berg. ex Triana, Trans. Linnean Soc. Bot., 28:148. 1871. SYNTYPES. ECUADOR: ad Guayaquil, Tafalla, *Ruiz s.n* (syntype: B [probably destroyed; photos at F, US]); at radices montis Chimborazo, *Spruce 6232*, *6233*. [syntypes: K].

Hemiepiphyte; young stems quadrate to flattened, internodes 1.5–4(–10) cm long, occasionally swollen and with domatia; leaves 5-nerved, 9–14 cm long, petioles vaginated; flowers 6-merous, anthers with a dorsal connective appendage; style with a few glandular trichomes at the base, stigma capitate.

Colombia, Ecuador, primary forests, 50–2500 m.

***Blakea subvaginata** Wurdack, Phytologia, 43:347. 1979. TYPE: ECUADOR. Tungurahua: Río Negro, shore of Río Pastaza, 1200 m, 12 Nov 1955, *E. Asplund 18393* (holotype: US; isotypes: NY, S)

Hemiepiphyte; young stems quadrate, internodes 1.5–4 cm long, occasionally swollen and with domatia; leaves 5-nerved, 15–23 cm long, petioles vaginated; flowers 6-merous, anthers without a dorsal connective appendage; style glabrous, stigma puctate to slightly expanded.

Ecuador, cloud forests, 1200–2000 m.

CLIDEMIA: ca. 210–220 species, 27 myrmecophites. The myrmecophitic species of *Clidemia* were last revised by Gleason (1931), but since then several new taxa have been described (Wurdack 1955, 1957, 1961, 1964, 1987; Almeda 2004), and others that were known only from a handful of specimens have been better collected. Almeda (2004) recently described five species of mymecophytic *Clidemia* and in this same publication included a list of 26 species known to have ant domatia. One species of *Clidemia* has ants inhabiting the base of a concave petiole (*C. ferox*). The remaining myrmecophitic species of *Clidemia* can be subdivided into two groups based on their domatia; domatia located at the base of the petiole, often partially fused to the stem, and domatia at the base of the leaf blade and/or the apex of the petiole. Both groups are in need of a revision and comparison with closely related species that lack domatia.

Clidemia acostae Wurdack, Phytologia, 38:299. 1978. TYPE: ECUADOR: Imbabura, entre Pajón y Cachago, 600 m, 2 Jun 1949, *Acosta-Solís 12722* (holotype: F).

Shrub to 1 m tall; stems densely pubescent, the trichomes reflexed 6–10 mm long; leaves isomorphic to slightly anisomorphic, 12–24 cm long, 7-plinerved, petioles 3–8 cm long; domatia present on both leaves of each node (rarely absent in the smaller leaf), 1–1.7 cm long, immersed in the leaf blade, the base usually projecting into the petiole; flowers 5-merous, stigma punctiform.

Colombia, Ecuador, 400–800 m.

Clidemia allardii Wurdack, Phytologia, 7:240. 1960. TYPE: PERU. San Martín: near cliffs atop of wooded ridge E of Tingo Maria, 625–1100 m, 30 Oct 1949–19 Feb 1950, *H. A. Allard 21222* (holotype: US).

Clidemia allardii subsp. *maranonensis* Wurdack, Phytologia 9:425. 1964. TYPE: PERU. Amazonas: Bagua, along Quebrada Tambillo (below km 280 of Marañon rd), above Cascadas de Mayasi, 425–525 m, 14 Sep 1962, *Wurdack 1993* (holotype: US; isotypes: F, K).

Shrub, up to 2.5(–3) m tall; stem and petiole setae up to 6 mm long, in part glandular, yellowish to reddish, also with dense barbellate trichomes 0.5 mm long; leaves 5–7-nerved, base cordate, petioles 4–14 cm; domatia at the base of the petiole, 7–12 mm long, absent from some nodes; inflorescences cymose less than 6 cm long; flowers 4-merous, hypanthia setose, petals white. Fig. 2A–B.

Colombia, Ecuador, Peru, Brazil, secondary forests and gaps, 200–900 m.

Clidemia allardii, *C. crenulata*, and *C. tococoidea* all have domatia at the base of long petioles and short cymose inflorescences, differing only on the type and density of the indementum, and to a lesser degree in the size of the petals. Most specimens can be easily assigned to one of the three species, but some individuals, especially in Colombia, seem to be intermediate between *C. crenulata* and *C. allardii*. The two subspecies are distinguished by inflorescence morphology (branched in the typical subspecies and compact in *C. allardii* subsp. *maranonensis*), but there are several intermediate collections and the differentiation might not be necessary.

Clidemia ayangannensis Wurdack, Brittonia, 39:161, f. 2. 1987. TYPE: GUYANA: Upper Mazaruni River Basin, Mt. Ayanganna along NE side, 2 Aug 1960 *S. S. Tillett 44998* with *C. L. Tillett* (holotype: US; isotypes: K, NY).

Shrub to 70 cm tall; stems and petioles pubescent, the trichomes eglandular and glandular, 2–3(–5) mm long; leaves anisomoprphic, the larger ones 14–20 cm long 5(–7)-plinerved, base broadly acute to obtuse, the smaller leaves up to 50% reduced; domatia present on both leaves of each pair at the apex of the petiole, extending up to ½ into the base of the leaf, oblong to fusiform, 0.8–2.5(–3) cm long; flowers 5-merous, stigma capitate.

Guyana, forests 600–1200 m.

****Clidemia ciliata** Pav. ex D. Don, Mem. Wernerian Nat. Hist. Soc., 4(2):309. 1823. TYPE: PERU, *Pavón s.n.* (holotype: BM; isotype B [destroyed]).

Shrubs up to 3 m tall; stems terete, pubescent, the trichomes less than 3 mm long; leaves 7–23 cm long, (5–) 7–9-nerved, cordate; flowers 4-merous, stigma punctate. Fig. 2D–E.

C. ciliata *var.* **elata** (Pittier) L. Uribe, Caldasia, 9(43):238. 1965. *Clidemia elata* Pittier, Bol. Soc. Venez. Cie. Nat. 11 (70): 21. 1947. TYPE: VENEZUELA. Mérida: 1700 m, 26 Jan 1928, *H. Pittier 12744* (holotype: US).

Leaf abaxial pubescence of stellate hairs

Honduras, Nicaragua, Costa Rica, Panamá, Colombia, Venezuela, borders of forests and secondary vegetation, 300–1600(–2100) m.

C. ciliata *var.* **testiculata** (Triana) L. Uribe, Caldasia, 9:238. 1965. *Calophysa testiculata* Triana, Trans. Linnean Soc. Bot., 28:140. 1871. *Maieta testiculata* (Triana) Cogn., in Mart., Fl. Bras., 14(4): 463. 1888. *Clidemia testiculata* (Triana) Gleason, Bull. Torrey Bot. Club, 58: 80–81. 1931. TYPE: COLOMBIA: 1851–1857, *Triana s.n.* (holotype: G).

Clidemia cymosa Gleason, Bull. Torrey Bot. Club, 52:455. 1925. Type: COLOMBIA, Meta: Villavicencio, 500 m, 26–31 Aug 1917, *Pennell 1510* (holotype: NY).

Leaf abaxial pubescence of simple setae.

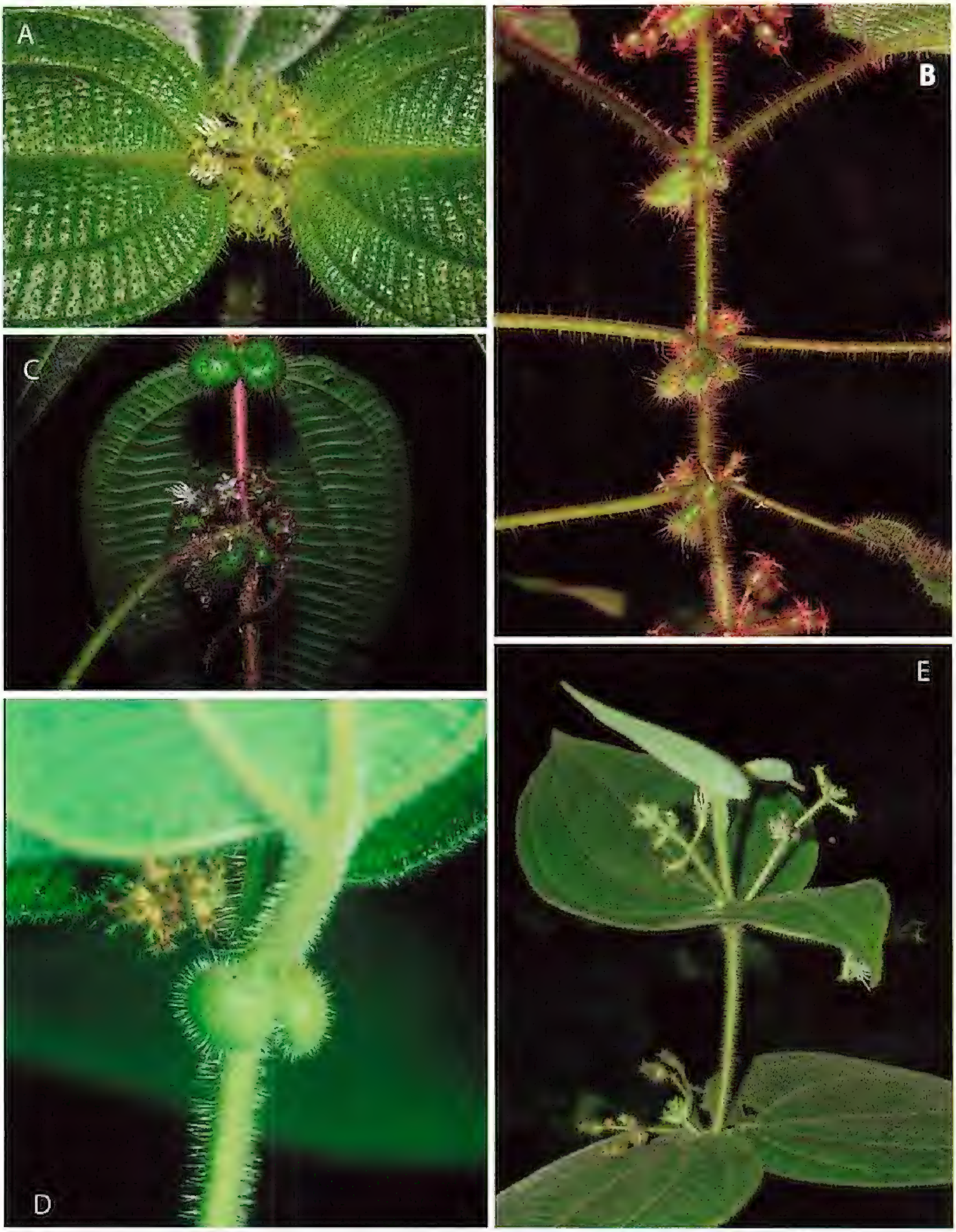


FIGURE 2. A. *Clidemia allardii*, leaves and inflorescence; B. *Clidemia allardii* stem, with paired domatia at the base of the petioles; C. *Clidemia crenulata* stem with inflorescence and domatia at the base of the petioles; D. *Clidemia ciliata* domatia; E. *Clidemia ciliata*, terminal branch. (photos: A-B, Mac Alford; C, Ricardo Kriebel; D-E, Fabián A. Michelangeli).

Colombia, Venezuela, 300–1800 m.

Clidemia ciliata belongs to a complex group, highly variable in petiole and leaf size, inflorescence morphology and size and pubescence of both vegetative and reproductive organs. This group includes the different varieties of *C. ciliata* (including two varieties that lack domatia; *C. ciliata* var. *ciliata* and *C. ciliata* var. *grandifolia* Cogn.), as well as *C. pilosa* and other taxa not bearing domatia such as *C. impetiolaris*. These taxa were evaluated by Gleason (1950) and by Uribe (1960), who arrived at different conclusions. More material is now available and probably should be re-evaluated.

Clidemia collina Gleason, Phytologia, 3:359. 1950. TYPE: PANAMÁ. Coclé: El Valle, *Allen 1820* (holotype: MO).

Shrub to 2 m tall; stems setose, the trichomes somewhat retrorse, simple, 4–8 mm long; leaves isomorphic or nearly so, 9.5–21 cm long, 7–11-plinerved, the adaxial surface setose; domatia fusiform, 2.5–8 cm long at the base of the blade and extending into the apex of the petiole; flowers 5-merous, stigma capitellate.

Panamá, forests 50–1200 m.

Clidemia crenulata Gleason, Bull. Torrey Bot. Club, 72(5):478. 1945. TYPE: COLOMBIA. El Valle: La Trojita, 5–50 m, *Cuatrecasas 16534* (holotype: NY; isotype: F).

Maieta tococoidea var. *watsonii* Cogn., Monogr. Phanerog., 7:979. 1891. TYPE: In Guatemala ad "Chocon Plantation": *S. Watson s.n.* (holotype not seen).

Herb to slender shrub, up to 1.5 m; stem and petiole setae up to 6 mm long, yellowish to reddish; leaves 7–9-nerved to slightly (less than 1 cm) plinerved, base acute to slightly cordate, petioles 4–10 cm; domatia at the base of the petiole, 7–14(–22) mm long, absent from some nodes; inflorescences cymose less than 2 cm long, peduncles > 10 mm long; flowers 4-merous, hypanthia setose, petals white. Fig. 2C.

Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, Colombia, Ecuador. Primary and secondary forests, 0–900 m.

See note under *Clidemia allardii*.

Clidemia ferox Gleason, Phytologia, 1:175. 1935. TYPE: BRAZIL. Amazonas: Humayta, between Monte Cristo and Santa Victoria on Río Ipixuna, 15–17 Nov 1934, *B. A. Krukoff 7262* (holotype: NY; isotypes: F, K, NY, US [2]).

Shrubs up to 5 m tall; leaves 3–5-nerved, 6–15(–20) cm long; domatia formed by concave and swollen (but not hollow) petiole bases; flowers 6-merous, hypanthium 10 mm long, densely setose. Fig. 1E.

Brazil, lowland evergreen forests, 100–200 m.

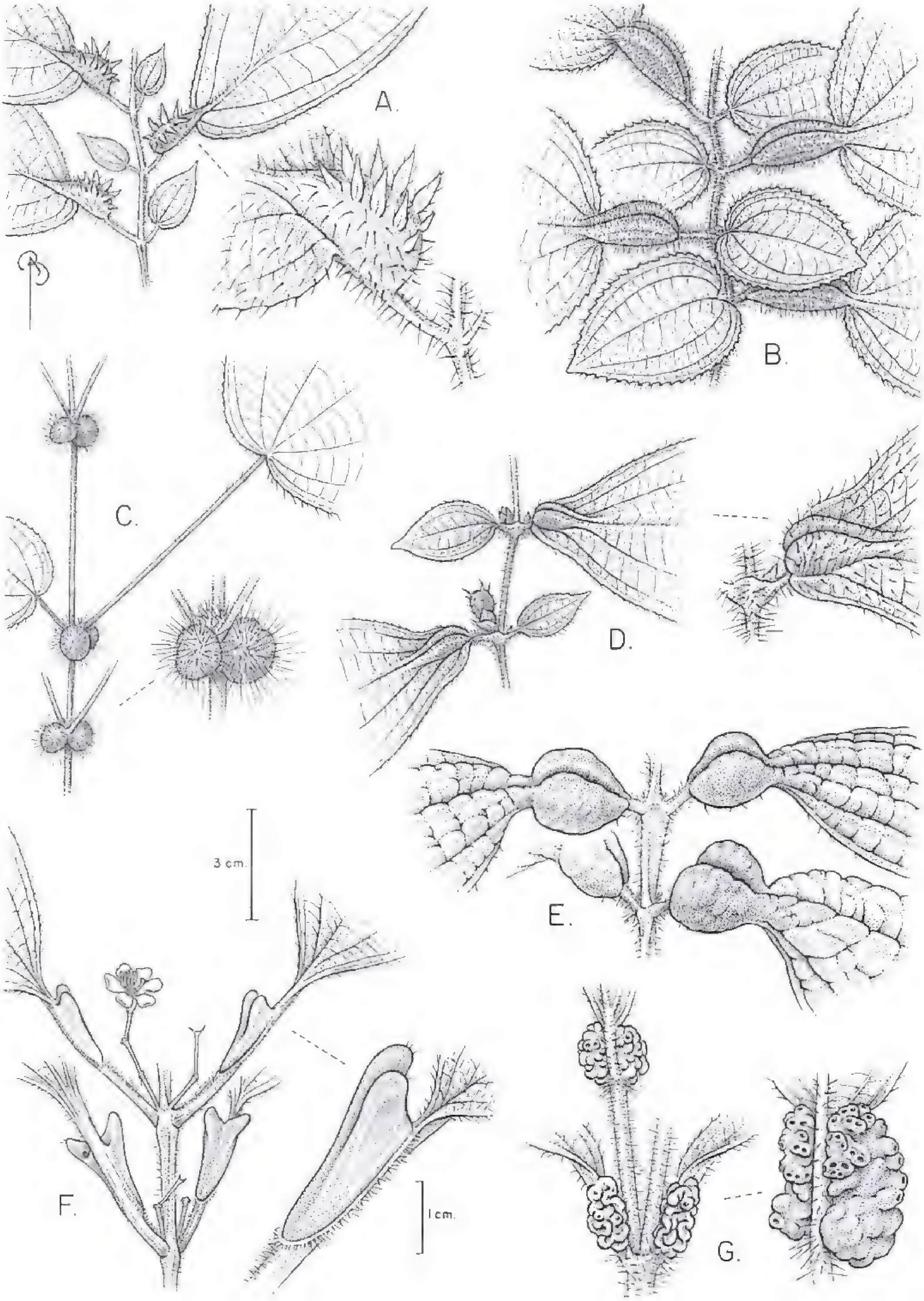
Clidemia foliosa Gleason, Bull. Torrey Bot. Club, 58:84–85. 1931. TYPE: PERU. Loreto: Timbuchi on the Río Nanay, *Ll. Williams 933* (holotype: NY; isotype: F).

Shrub up to 1 m; leaves anisomorphic, the smaller one less than ⅙ the size of the larger one, cordate; petioles in larger leaves < 1 cm long, petioles in smaller leaves > 8 mm long; domatia present only in the larger leaves, free from the leaf blade, ovoid, 2.5–4 cm long, bearing along the medial dorsal line 2–9 leaf like appendages 2–6.5 mm long; flowers 5-merous. Fig. 3A.

Peru, forests 100–300 m.

See note under *Clidemia heterophylla*.

Clidemia folsomii Almeda, Proc. California Acad. Sci., ser. 4, 55:101. 2004. TYPE: PANAMÁ. Veraguas: along trail to summit of Cerro Tute about ½ mile above the Escuela Agricultura Alto


A.
B.
C.
D.
E.
3 cm.
F.
1 cm.
G.

Piedra near Santa Fe, 29 Feb 1989, *F. Almeda et al. 6488* (holotype: CAS; isotypes: AAU, CAS, INB, MEXU, MO, PMA).

Shrubs up to 2 m tall; stems terete, pubescent, the trichomes spreading 1–2.5 mm, often glandular; leaves slightly dimorphic, 7–9-nerved or plinerved, both bearing domatia that run from the base of the leaf to the apex of the petiole, elongate, 3.5–7.5 cm long; inflorescences axillary, 6–13 cm long; flowers 5-merous; stigma punctiform.

Panamá, 800–1300 m.

Clidemia heptamera Wurdack, Mem. New York Bot. Gard., 10:179. 1964. Type: GUYANA: Mt. Ayanganna, Pakaraima Mountains, 5–6 Feb 1955, *B. Maguire, W. M. C. Bagshaw & C. K. Maguire 40752*. (holotype: US; isotpyes K, NY, U).

Shrub up to 2 m tall; leaves anisophyllous, the large ones 11–20 cm long, 5–7(–9)-nerved, petioles 0.2–2.5 cm long, the smaller leaves 50% reduced; domatia on both leaves of each pair, rarely only on the large leaf, 1.5–3 cm long, oblong to fusiform, at the apex of the petiole, occasionally barely extending into the base of the leaf blade; inflorescences in the upper axils, 1–2 fasciculate, with 1–2(–4) flowers, (6–)7-merous. Fig. 3B.

Venezuela, Guyana, primary forests 500–1500 m.

Clidemia heterophylla (Desr.) Gleason, Bull. Torrey Bot. Club, 58:85. 1931. *Melastoma heterophylla* Desr., Lam. Encyc. 4:34. 1796. *Tococa heterophylla* (Desr.) D. Don, Mem. Wernerian Nat. Hist. Soc., 4:305. 1823. *Maieta heterophylla* (Desr.) DC., Prodr., 3:166. 1828. *Calophysa heterophylla* (Desr.) Triana, Trans. Linnean Soc. Bot., 28:140. 1871. Type: PERU: 1778–88, *Ruiz & Pavon 16/47*. (holotype: MA n.v.).

Shrub up to 1.5 m; leaves anisomorphic, the smaller one less than ⅙ the size of the larger one, cordate; petioles in larger leaves < 1 cm long, petioles in smaller leaves > 8 mm long; domatia present only in the larger leaves, free from the leaf blade, ovoid, 0.7–1.2 cm long; inflorescence peduncle > 1.5 cm long; flowers 5-merous, hypanthia densely setose.

Colombia, Ecuador, Peru, Bolivia, Brazil, primary forests 150–1000 m.

Clidemia heterophylla forms a group with *C. foliosa, C. inobsepta* and *C. sprucei*, all anisophyllous and with the smaller leaf cordate and almost sessile. Wurdack believed that there might be more species in this group (Wurdack, 1980), but without a complete revision this is difficult to assess.

Clidemia inobsepta Wurdack, Mem. New York Bot. Gard., 16:37, f. 4a–e. 1967. Type: ECUADOR. Santiago-Zamora: "Oriente", Cordillera Cutucú, 2000–2300 ft. 0° 40' S 78° W, 17 Nov 1942, *W. H. Camp E-1051*. (holotype: US; isotype: NY).

Shrub up to 1.5 m; leaves anisomorphic, the smaller one less than ⅙ the size of the larger one, cordate; petioles in larger leaves < 1 cm long, petioles in smaller leaves > 8 mm long; domatia present only in the larger leaves, free from the leaf blade, ovoid, 0.7–1.2 cm long; inflorescence < 3 cm long; flowers 5-merous, ovary inferior. Fig. 4D.

Colombia, Ecuador, Peru, Brazil, primary forests, usually near ravines, 100–1200 m.

See note under *C. heterophylla*.

Figure 3. Foliar domatia of Neotropical Melastomataceae. A. *Clidemia foliosa* with domatia at the apex of the petiole, showing foliose appendages and anisophylly; B. *Clidemia heptamera*, with domatia at the apex of the petiole and anisophylly; C. *Clidemia tococoidea* with domatia at the base of the petiole; D. *Maieta guianensis* with domatia completely immersed in the leaf blade and anisophylly; E. *Tococa guianensis* with domatia at the apex of the petiole; F. *Tococa macrophysca* with domatia at the apex pf the petiole and with horn-like processes; G. *Tococa spadiciflora* with verrucose domatia at the apex of the petiole. Scale bar = 3 cm for habit or general views, and = 1 cm in details to the right of general view. (A from *Williams 1058*, B from *Hanh 3391b*, C from *Palacios 2591*, D from *Prance 1992*, E from *Maguire 33647*, F from *Clark 6806* and *Michelangeli 439*, G from *Clark 6806*; all specimens at NY).

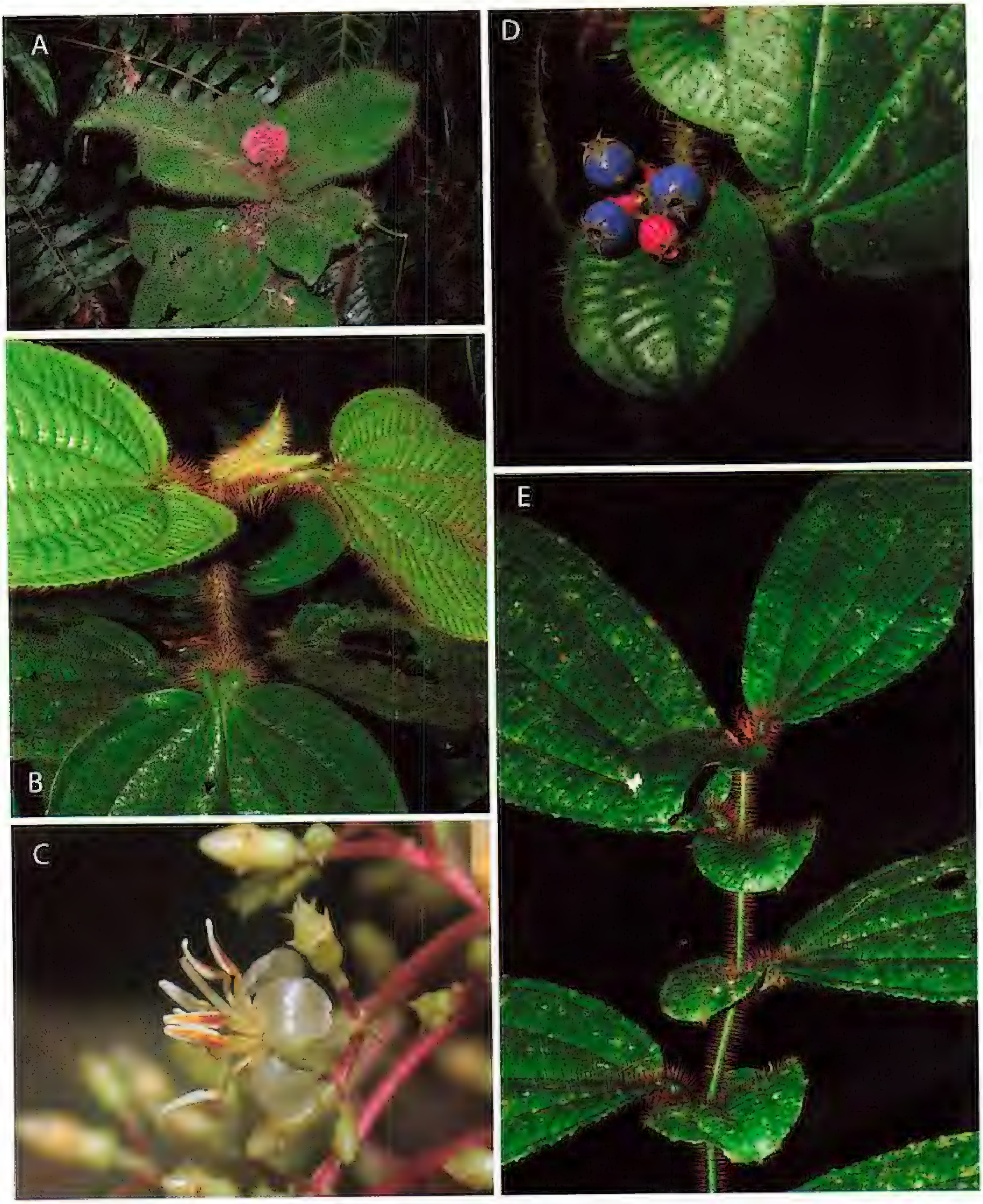


FIGURE 4. A. *Clidemia spectabilis*, habit; B. *Clidemia setosa* branch with foliar domatia; C. *Clidemia setosa* flower; D. *Clidemia inobsepta* infrutescence and anisophyllous leaf pair, the larger leaf with a domatium at the base of the blade; E. *Clidemia sprucei* branch. (photos: A-B, Ricardo Kriebel; C,E, Fabián A. Michelangeli; D, Douglas Daly).

Clidemia juruensis (Pilg.) Gleason, Bull. Torrey Bot. Club, 58:84. 1931. *Maieta juruensis* Pilg. Verhandlungen des Botanischen Vereins für die Provinz Brandenburg und die Angrenzenden Länder 47: 178. 1905. Type: BRAZIL. Acre: Jurua–Miry [sic], May 1901, *Ule 5449* (holotype: B [probably destroyed]; isotypes: K, MG).

Shrub to 2 m tall; stems and petioles pubescent, the trichomes eglandular and glandular, 2–3 (–5) mm long; leaves isomorphic, 10–22 cm long, 3–5-nerved, base acute; domatia present on both leaves of each pair at the apex of the petiole not extending into the base of the leaf, oblong 0.8.–1.5 cm long; flowers 5-merous, stigma slightly expanded.

Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia, forests 100–400 m.

Clidemia killipii Gleason, Bull. Torrey Bot. Club, 68:252. 1941. Type: COLOMBIA, Chocó: Corcovada region, upper Río San Juan, ridge along Yeracüí Valley, Alt. 200–275 m, 24–25 Apr 1939, *E. P. Killip 35249* (holotype: NY; isotypes: F, US).

Shrubs; leaves isomorphic, 5(–7)-nerved to shortly plinerved, the domatia free from the leaf blade, 1.3–2.2 cm long, deeply corrugated and with large pores throughout the surface; inflorescence an axillary (rarely terminal) panicle 12–18 cm long; flowers sessile, 5-merous, petals white to pale pink.

Colombia (Chocó), in primary forests 0–500 m.

See note under *Tococa spadiciflora.*

Clidemia lanuginosa Almeda, Proc. California Acad. Sci., ser. 4, 55:107. 2004. Type: PANAMÁ. Bocas del Toro: Fortuna Dam area along continental divide trail bordering Chiriquí province, 1200–1300 m, 10 Mar 1988, *F. Almeda et al. 6070* (holotype: CAS; isotypes: INB, MO, PMA).

Shrub up to 2 m tall; leaves isomorphic to slighty dimorphic, 8.5–22 cm long, 7–9-plinerved; domatia elongate, 2.5–5.5 cm long, completely immersed in the leaf blade; inflorescence terminal early in development, but becoming lateral by overtopping of the axillary bud, 2–8 cm long; flowers 4(–5)-merous; ovary inferior.

Panamá, primary forests, 300–1450 m.

Clidemia myrmecina Gleason, Phytologia, 3:360. 1950. Type: COLOMBIA. Antioquia: N of Dabeiba, along road to Turbo, 300–350 m., 25 Feb–1 Mar 1942, *R. D. Metcalf 30182, with J. Cuatrecasas* (holotype: UC; isotypes: NY, US).

Slender shrubs up to 1 m tall; stems setose, the trichomes reflexed, 3–6 mm long; leaves isomorphic or nearly so, 11–27 cm long, adaxial surface setose, 5–7-nerved; domatia elongated, 2–3.5 cm long; at the apex of the petiole, and extending up to ⅓ into the leaf blade; inflorescences 1.5–2.5 cm long; flowers 5-merous.

Panamá, Colombia, forests, usually near ravines, 100–1200 m.

Clidemia neblinae Wurdack, Mem. New York Bot. Gard., 10:45, fig 33 A, B. 1961. Type: VENEZUELA. Amazonas: Cerro de la Neblina, Río Yatua: 6–8 km S of Camp 3, Alt. 1400–1600 m., 24 Dec 1953, *B. Maguire 36862 with J. J. Wurdack & G. S. Bunting* (holotype: NY; isotype: K).

Shrubs or treelets to 6 m tall; leaves 20–35 cm long; domatia present at the base of the petiole, partially fused to the stem, ovoid to saccate, 1–1.5 cm; inflorescence terminal, 10–15 cm long; flowers 5-merous.

Venezuela, in foothills of tepuis, 1400–1600 m.

***Clidemia pilosa** Pav. ex D. Don, Mem. Wernerian Nat. Hist. Soc., 4:308. 1823. *Calophysa pilosa* (Pav. ex D. Don) Triana, Trans. Linnean Soc. Bot., 28:140. 1871. *Maieta pilosa* (Pav. ex D. Don) Baill., Histoire des Plantes, 7:19, f. 27. 1880. Type: PERU: 1778–88, *Ruiz & Pavón 15/10* (holotype: BM; isotype MA n.v.).

Staphidiastrum impetiolare Naudin, Ann. Sci. Nat., Bot., sér. 3, 17(5):329. 1851. *Clidemia impetiolaris* (Naudin) Cogn., Monogr. Phanerog. 7:1016. 1891. Type: PERU: 1787, *Ruiz & Pavon s.n.* (holotype: B [probably destroyed]).

Shrub up to 1.5 m tall; stem and petiole trichomes up to 3 mm long, often glandular; leaves cordate, 7–9-nerved, petioles 0.5–1.0 cm long; domatia developing unilaterally, ovoid, up to 1 cm long; flowers 4-merous.

Colombia, Venezuela, Ecuador, Peru, Bolivia, 600–1900 m.

See note under *Clidemia ciliata*.

***Clidemia pubescens** Gleason, Bull. Torrey Bot. Club, 58:82. 1931. Type: COSTA RICA. Salamanca [now in PANAMÁ, Bocas del Toro]: forêts de la Boca de Zhorquin, Mar 1894, *Tonduz 8574* (holotype: US; isotype: F).

Herb to slender shrub, up to 0.7 m tall; stem trichomes 2–12 mm long, eglandular, retrorse; leaves isomorphic to moderately anisomorphic 8.5–21 cm long, the smaller leaf up to 30% reduced, base cordate, 5–7(–9)-plinerved, more rarely basally nerved, the adaxial surface slightly bullate, the projections ending in trichomes 1–15 mm long, thickened towards the base, simple; domatia (when present) at the apex of the petiole, varying from ⅘ immersed in the leaf blade to completely free, 0.9–2.5 cm long, ovoid to oblong, setose; inflorescences pseudoaxillary, erect, up to 10 cm long, pedunculate; flowers 4–5-merous, petals pink to light red.

Costa Rica, Panamá, near streams in primary and secondary forest 100–1300 m.

Clidemia pubescens and *C. setosa* are two closely related and variable species and sometimes difficult to differentiate in herbarium material (although inflorescence orientation and petal color make it much easier in the field).

Clidemia rodriguezii Almeda, Proc. California Acad. Sci., ser. 4, 55:114. 2004. Type: COSTA RICA. Cartago: Cantón de Paraíso, cuenca del Reventazón, Orosí, entrada a Tarsito, aprox, 3 km después del cruce hacia la estación Tapantí, 1400–1600 m, 15 Apr 1988, *A. Rodríguez et al. 3239* (holotype: INB; isotypes: CAS, CR, MO, NY, US).

Herbs or small shrubs, up to 1.5 m tall. Stems quadrangular, winged; leaves 7-nerved, isomorphic or nearly so; domatia at the base of the leaf blade, less than 1 cm long; inflorescences axillary, in congested dichasia; flowers 4-merous, petals white.

Costa Rica. forests 700–1400 m.

The domatia of this species are particularly small, and careful examination of all specimens studied failed to yield any ants. Almeda (2004) had earlier suggested that these might be mite-domatia.

Clidemia setosa (Triana) Gleason, Bull. Torrey Bot. Club, 58:82. 1931. *Calophysa setosa* Triana, J. Bot., British and Foreign 5: 209. 1867. *Maieta setosa* (Triana) Cogn., Fl. Bras., 14(4): 462. 1888. Type: NICARAGUA: Chontales, *B. Seemann s.n.* (holotype: not found)

Clidemia trichogona Gleason, Brittonia, 3:117. 1939. Type: COSTA RICA. Alajuela: La Peña de Zarcero. Cantón Alfaro Ruiz, 1525 m., Jul 1938, *Austin Smith 4995* (holotype: NY; isotype: NY).

Herb to slender shrub, up to 1.5 m tall; stem trichomes 8–25 mm long, eglandular, retrorse; leaves isomorphic or nearly so, 7.5–25 cm long, base cordate, 5–7(–9)-nerved, the adaxial surface glabrescent to sparsely setose, the trichomes up to 7 mm long, simple; domatia at the apex of the petiole, usually free from the leaf blade, rarely extending up to ⅕ into the lamina, 0.9–2.5 cm long, ovoid to oblong, setose; inflorescences pseudoaxillary, perpendicular to the stem in the lower nodes, reflexed in the upper nodes, on a peduncle 2–7 cm long; flowers 4(–5)-merous, petals white to pale pink. Fig. 4B–C.

Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, primary forests near streams, 100–1400 m.

See note under *Clidemia pubescens*.

Clidemia spectabilis Gleason, Bull. Torrey Bot. Club, 58:83–84. 1931. TYPE: COSTA RICA: El Muñeco, 1500 m, 19 Jun 1925, *Stork 2717* (holotype: F).

Maieta setosissima Suess., Bot. Jahrb. Systematik, Pflanzengeschichte und Pflanzengeographie, 72(2):277–278, t. 4, f. 9. 1942. TYPE: Costa Rica: Orósi, 14 Mar 1932, *Kupper 772* (holotype: M; isotypes: M[4]).

Herb to slender shrub, up to 1 m tall; stems pubescent, the trichomes eglandular, up to 18 mm long; spreading, becoming retrorse; leaves (5–)7–9-plinerved, leaves slighty dimorphic, surface bullate, the abaxial surface with eglandular trichomes up to 22 mm long; domatia completely immersed in the leaf blade, 1.2–3.5 cm long, occasionally missing from the smaller leaf of each pair; inflorescences umbelliform, on a peduncle 5–9 cm long, erect or more rarely decumbent; flowers 5-merous, petals white to pink. Fig. 4A.

Nicaragua, Costa Rica, Panamá, cloud forests 700–1400 m.

Clidemia sprucei Gleason, Bull. Torrey Bot. Club, 58:85. 1931. *Calophysa dentata* Triana, Trans. Linnean Soc. Bot., 28: 140. 1871. *Maieta dentata* (Triana) Cogn., Fl. Bras., 14(4): 465. 1888. TYPE: PERU: in montibus secus flumen Mayo prope Tarapoto, *Spruce 4441* (LECTOTYPE: K designated by Gleason, 1921). Not *Clidemia dentata* Pav. ex D. Don.

Shrub up to 1.5 m; leaves anisomorphic, the smaller one less than ⅕ the size of the larger one, cordate; petioles in larger leaves < 1 cm long, petioles in smaller leaves > 8 mm long; domatia present only in the larger leaves, free from the leaf blade, ovoid, 0.7–1.2 cm long; inflorescence < 3 cm long; flowers 4-merous, ovary ⅔ inferior. Fig. 4E.

Ecuador, Peru, Bolivia, Brazil, primary forests, often near ravines 200–900(–1200) m.

Gleason used the epithet "*sprucei*" when transferring this species to *Clidemia*, because there was already a previous homonym. See note under *C. heterophylla*.

Clidemia taurina Gleason, Phytologia, 3:360. 1950. TYPE: PANAMÁ. Bocas del Toro: collected on Old Bank Island, *H. von Wedel 1917* (holotype: MO).

Shrubs up to 0.7 m tall; stems pubescent, the trichomes eglandular, 4–14 mm long, spreading or retrorse; leaves 7-nerved, isomorphic, or slightly dimorphic (up to 20%), the adaxial surface glabrescent, rarely with eglandular trichomes up to 14 mm long; domatia at the apex of the petiole, occasionally projecting into the leaf blade, 1.5–2.5 cm long; inflorescences pseudoaxillary, umbeliform, up to 3 cm long; flowers 5-merous, petals white. Fig. 5A.

Costa Rica, Panamá, forests 100–500 m.

Clidemia tenebrosa Almeda, Proc. California Acad. Sci., ser. 4, 55:107. 2004. TYPE: PANAMÁ. Coclé: forested slopes above road leading to the continental divide, 700–850 m, 24 Jan 1989, *F. Almeda et al. 6392* (holotype: CAS; isotypes: MO, PMA).

Monopodial to few branched shrub, up top 3 m tall; leaves isomorphic, 22–44.5 cm long, 7–9-plinerved; domatia elongate, 4–7 cm long at the base of the blade, extending into the apex of the petiole; inflorescences axillary, 2–3.5 cm long; flowers 5-merous.

Panamá, primary forests 200–1100 m.

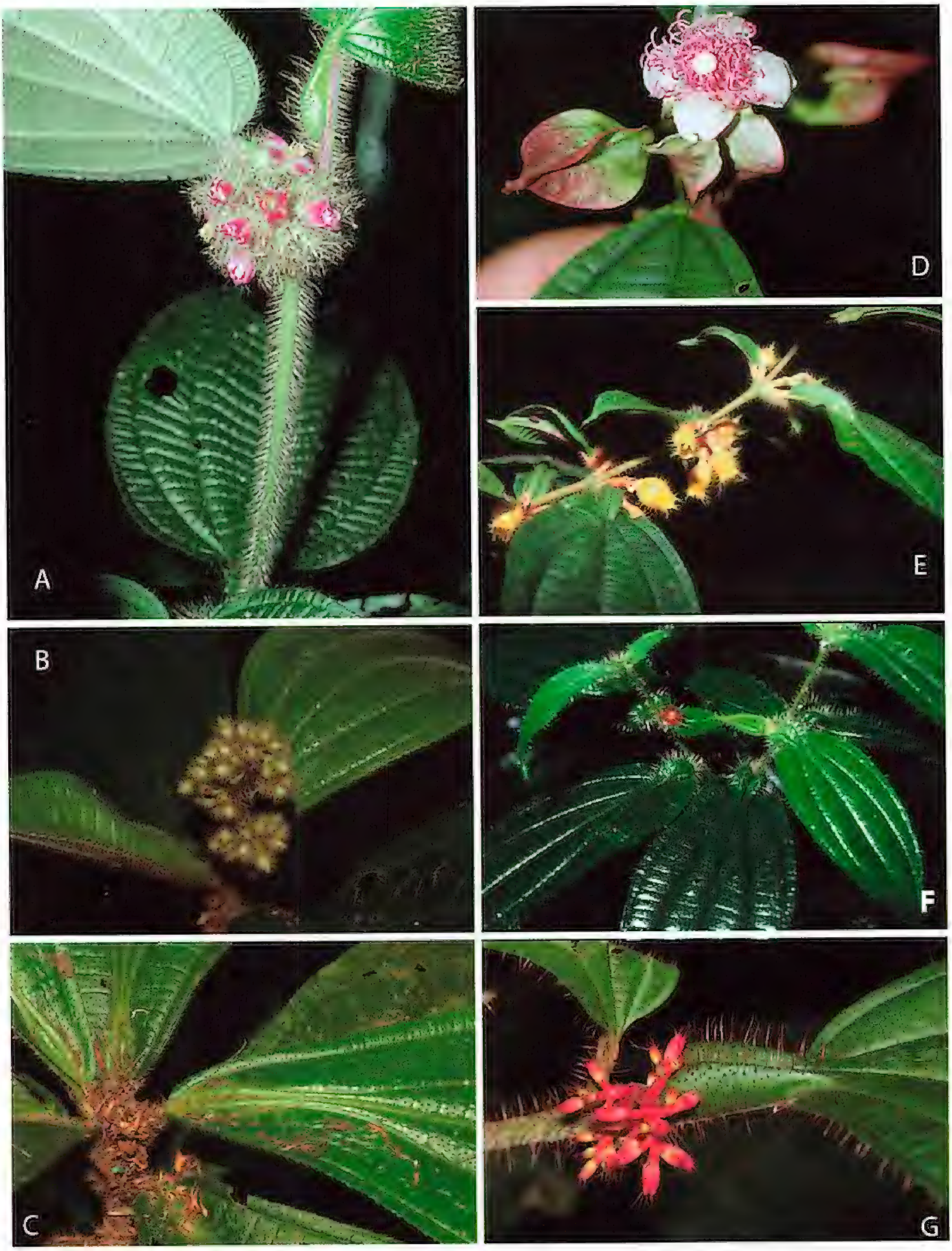


FIGURE 5. A. *Clidemia taurina* branch with inflorescence and petiolar domatia; B. *Conostegia setosa*, branch with young inflorescence; C. *Conostegia setosa*, detail of laminar domatia; D. *Conostegia inusitata* open flower and buds; E. *Maieta poeppigii* branch with young fruits and laminar domatia; F. *Tococa macrosperma* with young fruits and laminar domatia; G. *Tococa caquetana*, young inflorescence and petiolar domatia. (photos: A, D, Robin Foster; B-C, E-F, Fabián A. Michelangeli; G, Mac Alford)

Clidemia tococoidea (DC.) Gleason, Bull. Torrey Bot. Club, 58:81. 1931. *Calophysa tococoidea* DC., Prodromus Systematis Naturalis Regni Vegetabilis, 3:166. 1828. *Maieta tococoidea* (DC.) Cogn., Fl. Bras. 14(4):465. 1888. TYPES BRAZIL: *Ferreira s.n.* (holotype: P).

Shrub to 3 m tall; stems terete, pubescent, the trichomes simple or glandular, up to 4 mm long; domatia present at the base of the petiole, partially fused to the stem, ovoid to saccate, 10–22 mm long; leaves 5–7-nerved, petioles 2–6 cm long; flowers solitary, rarely on dichasia 1 cm long, 4–merous. Fig. 3C.

Colombia, Venezuela, Brazil, 100–800(-1500) m.

Central American material that was initially determined as *Clidemia tococoidea* really corresponds to *C. crenulata*. See note under *Clidemia allardii*. For a detailed discussion on the provenance of the type of *C. tococoidea* see Wurdack (1971).

Clidemia ventricosa Almeda, Proc. California Acad. Sci., ser. 4, 55:120. 2004. TYPE: PANAMÁ. Comarca de San Blas: El Llano-Cartí road, 19.1. km from Interamerican Hwy., 350 m, 5 Mar 1985, *G. de Nevers, et al. 4963* (holotype: CAS; isotypes: CAS, INB, KUNA, MEXU, MO, PMA).

Shrub up to 1 m tall; leaves isomorphic or nearly so, 11–23.5 cm long, the adaxial surface glabrous; domatia 1–2 cm long, ovoid, at the apex of the petiole, with trichomes 0.6–1.7 long; Inflorescence pseudoaxillary, 1.5–2 cm long; flowers 5-merous.

Panamá, forests 300–400 m.

Clidemia sp. A.

Guyana. This undescribed species of myrmecophitic *Clidemia* is known from only a handful of recently collected specimens from Guyana. It differs from *C. neblinensis* in that the former is 4-merous, while the latter has 5-merous flowers.

CONOSTEGIA: 50 species, 4 myrmecophites. *Conostegia* is characterized by its pleiostemonous flowers with a calyptrate calyx, and it is most likely monophyletic (Michelangeli et al. 2004). The genus was last monographed by Schnell (1996), but his dissertation has never been formally published. Two species have domatia in the leaf blades, while two have hollow stems. The two species with primary domatia were treated as the segregate genus *Florbella* by Schnell (1996) in his dissertation, with one of them being transferred from *Conostegia* and the second one as a new taxon, but this genus was never formally published and these taxa are treated here under *Conostegia*.

Conostegia dentata Triana, Trans. Linnean Soc. Bot., 28:99. 1871. TYPE: COLOMBIA. Chocó: In sylvis umbrosis, *Triana 4113* (holotype: not seen).

Conostegia hispida Gleason, Bull. Torrey Bot. Club 66(6):415–416. 1939. TYPE: ECUADOR. Esmeraldas: Parroquia de Concepción, 105 m, *Y. Mexia 8430* (holotype: NY; isotypes: BM, F, GH, MO, NA, UC, US [frag.]).

Shrub; domatia ⅔ immersed in the base of the leaf blade; flowers calyptrate, (5–)6(–8)-merous, stamens 19–28.

Panamá, Colombia, Ecuador, 0–300 m.

For a detailed discussion about the type see Schnell (1996).

Conostegia inusitata Wurdack, Phytologia, 16:170. 1968. TYPE: PERU. Loreto: Coronel Portillo, lower boquerón del Padre Abad, 480 m, 25 Jul 1964, *P.C. Hutchinson, J. K. Wright & R. M. Straw 6057* (holotype: US; isotypes: MICH, MO [2], NY, UC, USM).

Shrubs; branches tetragonal, with swollen hollow stems towards the nodes (primary domatia); flowers in bud with the calyx fused into a 1–5 cm long calyptra, 4-merous, stamens 44–96. Fig. 5D.

Perú, 500–1500 m.

Conostegia setosa Triana, Trans. Linnean Soc., 28:99. 1871. Type: COLOMBIA. Chocó: Cordillera Occidental, between Tuquerres and Barbacoas, *Triana 3940* (holotype: BM; isotypes: BR, K, P, W).

Cryptophysa setosa Standl. & J. F. MacBr., Publ. Field Mus. Nat. Hist., Bot. Ser., 4:244. 1929. *Conostegia hirsuta* Gleason, Phytologia 3:359. 1959. Type: PANAMÁ. Bocas del Toro: Buena Vista, Almirante, Jan–Mar 1929, *Cooper 219* (holotype: F; isotype: NY) non *Conostegia setosa* Triana.

Single stemmed shrub; leaves clustered at the apex; domatia immersed in the leaf base, fusiform; flowers calyptrate, 4–6-merous, stamens 13–17. Fig. 5B–C.

Costa Rica, Panamá, Colombia and western Venezuela, 0–1000 m.

Conostegia sp. A

Shrub; terete stems with hollow internodes (primary domatia); flowers calyptrate, (6–)7–8(–12)-merous, stamens 58–114.

Peru, 400–900 m.

This species was treated as *Florbella wurdackii* by Schnell (1996) in his dissertation. However, this species is not yet validly published, and the distinction between *Florbella* and *Conostegia* might be unnecessary.

Henriettella: 32 species, 1 myrmecophite. *Henriettella cuneata* is the only neotropical myrmecophite with cauline inflorescences. *Henriettella* is closely related to *Henriettea* and other cauliflorous taxa like *Bellucia*, *Loreya* and *Myriaspora* (Michelangeli et al. 2004; Penneys et al. 2004b).

Henriettella cuneata (Standl.) Gleason, Bull. Torrey Bot. Club, 58:75. 1931. *Maieta cuneata* Standl., Publ. Field Columbian Mus., Bot. Ser., 8:30. 1930. *Henrriettea cuneata* (Standl.) L.O. Williams, Fieldiana Bot., 29:565. 1963. Type: BRITISH HONDURAS [now BELIZE]: Middlesex, dense forest along mountain stream, alt. 75 m, 1 Sep 1929, *W.A. Schipp 320* (holotype: F; isotypes: BM, MO, NY).

Shrub to small tree; domatia immersed in the base of the leaf blade, barely extending into the apex of the petiole; inflorescences cauline, fasciculated; flowers 5-merous, petals with subapical teeth.

Belize, Guatemala, Nicaragua, Costa Rica, Panamá, Colombia, 0–150(–1000) m.

Maieta: 3 species, all myrmecophites. *Maieta* is a small genus with lateral inflorescences and is distinguished from *Clidemia* by its anthers with bilobed thecae prolonged below the connective. Twenty-seven species (and at least three varieties) have been described or transferred to this genus, with Gleason (1931) transferring most of them to *Clidemia* based on floral characters. Wurdack repeatedly recognized only three species (1964; 1973; 1980), although a formal revision was never made. In a statistical analysis of vegetative morphology of *Maieta*, Whiffin (1971) also mentioned three species, and recognized two varieties for *M. guianensis*. These two varieties were distinguished based on hypanthium and petal color, and pubescence. However, several intermediates seem to exist that makes recognition of the varieties difficult at best. Two of the species are widely distributed and one is endemic to the slopes of Cerro La Neblina on the border between Venezuela and Brazil.

Maieta guianensis Aubl., Hist. Pl. Guiane Françoise, 1:443, t. 176. 1775. *Tococa mayeta* (Aubl.) D. Don, Mem. Wernerian Nat. Hist. Soc., 4:305. 1823. *Melastoma mayeta* Willd., Sp. Pl. 2: 589. TYPE: FRENCH GUIANA: *Aublet s.n.* (holotype: BM, LINN-SM-782.35).

Majeta dispar Miquel, Linneana, 18:277. 1844. TYPE: SURINAME: Para, prope Bergendaal, *H. C. Focke 384* (holotype: U).

Maieta hypophysca DC., Prodr., 3:166. 1828. TYPE: BRAZIL: sylvis Brasiliae, *Martius s.n.* (holo type: M)

Myrmidone peruviana Cogn., Bot. Jahrb. Systematik, Pflanzengeschichte und Pflanzengeographie, 42:147. 1908. *Maieta guianensis* var. *peruviana* (Cogn.) Ule, Notizbl. Bot. Gart. u. Mus. Berlin-Dahlem, 6:368. 1915. TYPE: PERU: *Weberbauer 3662* (holotype: B [probably destroyed]; isotype: BR).

Maieta hispida Rusby, Mem. New York Bot. Gard., 7:315. 1927. TYPE: BOLIVIA: 1500 ft, 08 Dec 1921, *White 1839* (holotype: NY; isotype: NY).

Maieta guianensis var. *leticiana* Whiffin, Brittonia, 23:326. 1971. TYPE: BRAZIL. Amazonas: north of Marco, near the border with Colombia (at Leticia), 110 m, 5 Aug 1968, *T. Whiffin 83* (holotype: US; isotypes: COL, K).

Shrub, rarely branched; leaves dimorphic, the larger one with a domatia immersed in the leaf blade, the smaller one without domatia; inflorescences solitary or 2-flowered cymes, subtended by 2–3 pairs of bracteoles; flowers 5-merous, the hypanthium terete; stamens prolonged below the insertion, bilobed; stigma capitate. Fig. 3D.

Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Brazil, Bolivia, 0–500 (1200) m.

Maieta neblinensis Wurdack, Mem. New York Bot. Gard., 10:178. 1964. TYPE: VENEZUELA. Amazonas: Cerro de la Neblina, Rio Yatua, in talud forest between Camps 3 and 4, 700–900 m., 07 Nov 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 41993* (holotype: US; isotypes: NY, P, U, VEN).

Shrub, rarely branched; leaves dimorphic, the larger one with a domatia immersed in the leaf blade, the smaller one without domatia; inflorescences solitary or 2–5-flowered cymes, subtended by 1 pair of bracteoles; flowers 5-merous, the hypanthium with 10 glandular-ciliolate wings; stamens prolonged below the insertion, bilobed; stigma capitate.

Endemic to the foothills of Cerro La Neblina, Venezuela, 700–1200 m.

Maieta poeppigii Mart. ex Cogn., Fl. Bras., 14(4):464, t. 99. 1888. SYNTYPES. BRAZIL: sylvarum marginibus ad Ega prov. do Alto Amazonas, *Poeppig, 3025 p.p.* (B [destroyed], BR, P); BRAZIL. Para: Colares, *Poeppig, 3025 p.p.* (B [destroyed], BR, GOET [n.v.]); PERU: *Pavon s.n.* (n.v.); PERU: *Fielding s.n* (n.v.).

Shrub, rarely branched; leaves dimorphic, the larger one with a domatia immersed in the leaf blade, the smaller one without domatia; inflorescences 2–7-flowered cymes, subtended by 1 pair of bracteoles; flowers 5-merous, the hypanthium terete; stamens prolonged below the insertion, bilobed; stigma capitate. Fig. 5E.

Costa Rica (only at Isla del Coco), Colombia, Venezuela, Guyana, French Guiana, Suriname, Ecuador, Brazil, Peru, 0–500(–900) m.

Maieta poeppiggi was first mentioned by Triana (1871) in his treatment of the Melastomataceae, based on a Martius manuscript, but no formal description was made. The species was formally described in Cogniaux's (1888) treatment of the Melastomataceae for *Flora Brasiliensis*, based on the same manuscript by Martius.

MERIANTHERA: is a genus with three species in the tribe Merianieae. One species has hollow stems and has been reported to have ants.

Merianthera burlemarxii Wurdack, Phytologia, 55:133–134. 1984. TYPE: BRAZIL: Rio de Janeiro, garden of Roberto Burle Marx [but introduced from Espirito Santo, Mun. Colatina, Rio Doce, Vila Panca], 24 Sep 1983 (fl), *P. C. Hutchinson 8472* (holotype: RB; isotype: US).

Deciduos shrub up to 1 m tall with hollow and swollen stems, and adventitious roots. Flowers 5-merous, petals magenta, ovary inferior, fruit capsular.

Brazil, 500–850 m.

MICONIA: aprox. 1100 species, 4 myrmecophites. *Miconia* is a large paraphyletic assemblage with many other genera of the Miconieae derived from within it (Michelangeli et al., 2004; Goldenberg et al., 2008; Michelangeli et al., 2008). Four species have been found to house ants in hollow stems.

Miconia bailloniana J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13(4/1):388. 1941. *Pterocladon sprucei* Hook. f. ex Cogn., Fl. Bras., 14(4):209, pl. 45. 1886. TYPE: PERU: prope Tarapoto, Aug 1856, *Spruce 4312* (holotype: P). Non *Miconia sprucei* Triana.

Shrubs to small trees; stems quadrangular, with swollen hollow nodes; leaves 5-plinerved; flowers 4–5-merous, diplostemonous, the hypanthia winged. Fig. 1F.

Peru, 100–1500 m.

Miconia expansa Gleason, Bull. Torrey Bot. Club, 63:536. 1936. TYPE: PERU. Loreto: Pumayacu, between Balsapuerto and Moyobamba, 600–1200 m, Aug–Sep 1933, *G. Klug 3201* (holotype: NY; isotype: US).

Shrubs to small trees; stems quadrangular, winged, with swollen hollow nodes; leaves 5-plinerved; flowers 5-merous, diplostemonous, the hypanthia terete.

Peru, 1500–2000 m.

Miconia flaccida Gleason, Bull. Torrey Bot. Club, 58:226. 1931. TYPE: PERU. Junín: Eneñas, Pichis trail, 1600–1900 m, 30 Jun–2 Jul 1929, *Killip & Smith 25625* (holotype: NY; isotype: US).

Shrubs to small trees; stems quadrangular, with swollen hollow nodes; leaves 3-plinerved; flowers 5-merous, diplostemonous or pleiostemonous, the hypanthia terete to slightly 10-costate.

Peru, 1100–1900 m.

Miconia hospitalis Wurdack, Phytologia, 23:475. 1972. TYPE: PERU. Junin: Schunke Hacienda, above San Ramon, 1700–1800 m, Jul 1925, *C. Schunke A120* (holotype: US).

Shrubs to small trees; stems slightly quadrangular, becoming terete, with swollen hollow nodes; leaves 3-plinerved; flowers 5-merous, diplostemonous, the hypanthia terete.

Peru, 1500–2000 m.

OSSAEA: aprox. 100 species, one myrmecophite. *Ossaea* is a polyphyletic genus in urgent need of revision. It is characterized by flowers with acute petals, and as currently defined it can be distinguished from *Leandra* only by inflorescence position, which is terminal in *Leandra* and lateral in *Ossaea*, and the presence of an apical tooth in the petals, rounded or emarginate in *Clidemia*.

Ossaea bullifera (Pilg.) Gleason, Bull. Torrey Bot. Club, 58:260. 1931. *Leandra bullifera* Pilg., Verhandlungen des Botanischen Vereins für die Provinz Brandenburg und die Angrenzenden Länder 47: 169. 1905. Type: PERU: *Ule 6202* (holotype: B [probably destroyed]).

Shrub; leaves dimorphic, the larger one with ovoid domatia at the apex of the petioles; petioles 4–7 cm long; inflorescences axillary panicles; flowers 5-merous; petals acute.

Colombia, Ecuador, Peru, 100–1000 m.

TOCOCA: 49 species, 30 myrmecophites. The genus was recently monographed (Michelangeli, 2005), and since then two new myrmecophitic species have been described (Michelangeli, 2006). As currently circumscribed, *Tococa* is not monophyletic. *Tococa sensu stricto* has 36 species, 24 of them myrmecophites, including the genera *Myrmydone* and *Microphysca*. There are 11 species included as *insertae sedis*, six of them myrmecophites.

Tococa aristata Benth., J. Bot. (Hooker), 2:305. 1840. Type: BRITISH GUIANA [now GUYANA]: Sides of Creeks, *Schomburgk 458* (holotype: K; isotypes: NY, P).

Shrub; domatia ⅓–⅕ immersed in the leaf base; flowers 5-merous, petals orange to brownish yellow.

Venezuela, Guyana, Brazil, 250–1400 m.

Tococa bullifera Mart. et Schrank ex DC., Prodr., 3:165. 1828. Type: BRAZIL: *Martius 6332* (holotype: G [photos at F, NY]).

Tococa bullifera var. *leiocalyx* Cogn., Bol. Mus. Goeldi, 5(2):255. Type: PERU. Loreto: Maynas, Iquitos, 12 Aug 1906, *Ducke 7601*, (holotype: BR).

Tococa bullifera var. *glabrata* Cogn., Bol. Mus. Goeldi, 5(2):255. Type: BRAZIL. Pará: Tabatinga, 12 Oct 1904, *Ducke 6850*, (holotype: BR).

Tococa spruceana Cogn., in Mart., Fl. Bras., 14(4):443. 1888. Type: BRAZIL. Alto Amazonas: prope Panure ad Rio Uaupes, *Spruce 2568* (holotype: BR; isotypes: K[2], P).

Tococa ulei Pilg., Verh. Bot. Ver. Brand., 47:177. 1905. Type: PERU. Loreto: *Ule 6200*. (Holotype: B, destroyed [photos at F 16–3, NY]; lectotype: K, designated by Michelangeli (2001a); isotypes: G, L).

Shrub; domatia ovoid to elliptic, at the apex of the petiole, free from the leaf blade; inflorescence a terminal single-branched panicle; flowers 5-merous; ovary apex with a corona of setae.

Venezuela, Peru, Brazil, 50–250 m.

Tococa capitata Trail ex Cogn., in Mart., Fl. Bras., 14: 615. 1888. Type: BRAZIL: Alto Amazonas, ad Januaria secus río Purus, *Trail 288* (lectotype: K, designated by Michelangeli (2001), [photo at F, negative 94-2]; isolectotype: BR).

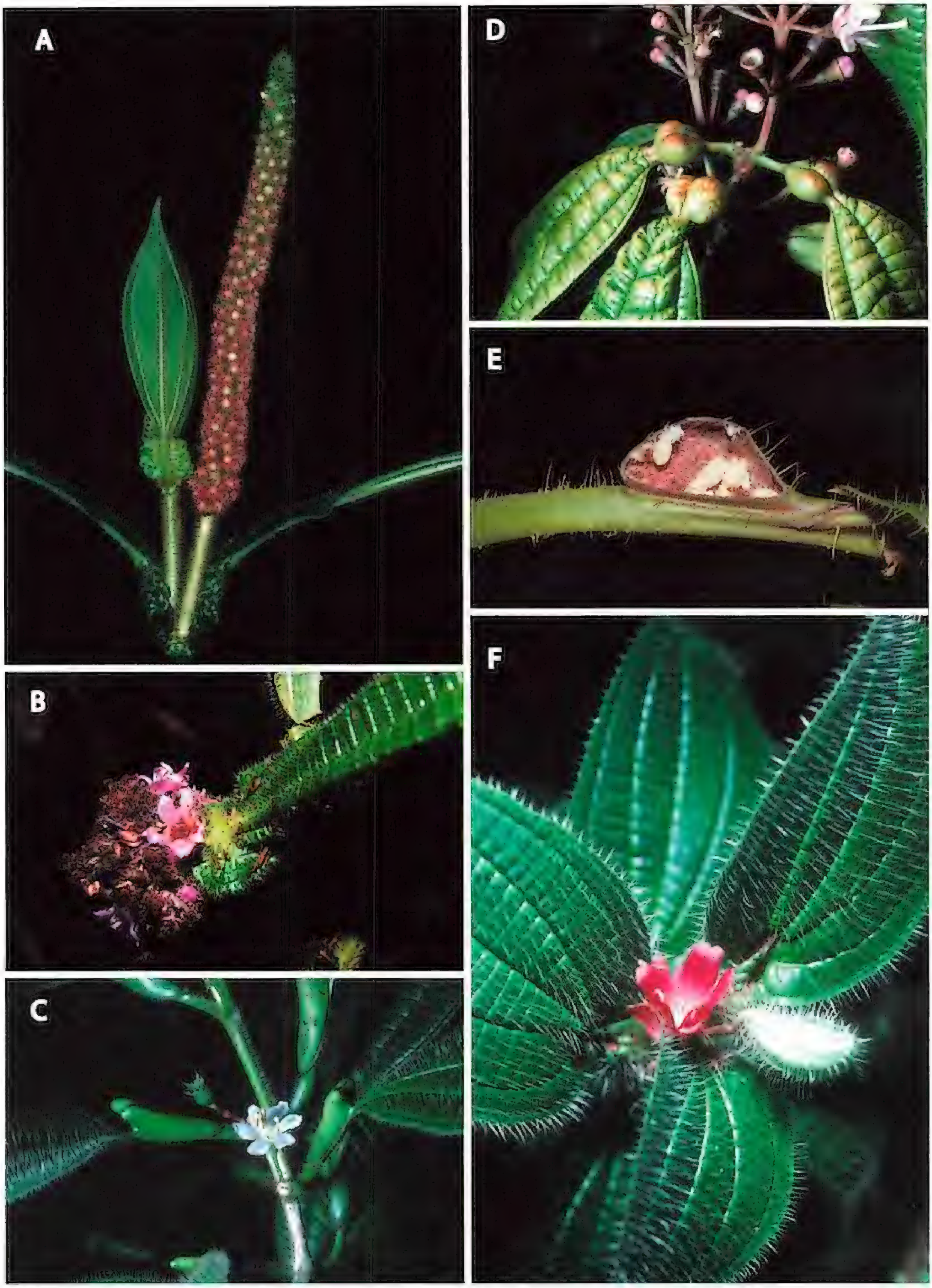
Erect shrubs; leaves with short petioles, domatia immersed in the leaf blade; inflorescences terminal condensed racemes; flowers 5-merous, anthers and fruits blue to purple. Fig. 6B.

Colombia, Peru, Brazil, along rivers and streams, 100–250 m.

Tococa caquetana Spruce, Trans. Proc. Soc. Edinburgh, 22:432. 1905. Type: COLOMBIA. San Jose, Río Putumayo, 3 Aug 1899, *Sprague 604* (holotype: US; isotypes: BM, K[3]).

Tococa micrantha Ule, Notizbl. Bot. Gart. Berlin-Dahlem, 6:364. 1915. Type: PERU. Loreto: Sep 1902, *Ule 6369* (holotype: B [destroyed, photo at F 13-5]; lectotype: K, designated by Michelangeli (2001); isotypes: F, G, GOE[n. v.], L).

Shrubs; leaves slightly dimorphic, domatia at the apex of the petiole, usually on both leaves of each pair; inflorescence a terminal panicle; flowers 5-merous, anthers white to yellow, with an orbi-


A
B
C
D
E
F

cular gland on the dorsal portion of the connective. Fig. 5G.

Colombia, Ecuador, Peru, Brazil, understory of primary forests, 200–1000 m.

Tococa carolensis Gleason, Amer. J. Bot., 19:746. 1932. TYPE: BOLIVIA. La Paz: San Carlos, near Mapiri, *Buchtien 976* (holotype: NY; isotypes: K, NY, US).

Shrubs; leaves dimorphic, the smaller ones ⅓–½ the length of the larger ones; domatia ovoid, at apex of the petiole, sometimes absent in the smaller leaf of each pair; flowers 6-merous, pleiostemonous; calyx dehiscing irregularly above the torus.

Peru, Bolivia, primary forests, 200–800 m.

Tococa caudata Markgr., Notizbl. Bot. Gart. Berlin-Dahlem, 9:1146. 1927. TYPE: PERU: Mittlere Marañon, Mundung der Apaga, in flutfreien Hochwald, 145 m. u. d M., 23 Dec 1924, *Tessman 4815* (holotype: B [Photo at NY], destroyed). NEOTYPE (designated by Michelangeli, 2001): PERU. Loreto: Río Nanay, 120 m, 4 Jan 1976, *Gentry, A. & Ayala, F. 15549* (neotype, F; isolectotypes: AMAZ, MO, NY).

Shrubs; domatia immersed in the leaf blade; inflorescences terminal panicles with 30–70 flowers; flowers 5-merous, anthers and fruits blue to purple; ovary completely inferior.

Colombia, Peru, Brazil, in seasonally flooded areas along the Amazon and tributaries, 100–250 m.

***Tococa ciliata** Triana, Trans. Linnean Soc. Bot., 28:133. 1871. TYPE: VENEZUELA. Amazonas: Caño Pimichín, *Spruce 3715* (holotype: K [photo at F 92-4]; isotypes: BR, P).

Shrub or slender tree; leaf margin ciliolate, occasionally with domatia completely immersed in the base; flowers 5-merous.

Venezuela, Brazil, 100–300 m.

This species has not yet been collected in Colombia, but it certainly grows there in the Guainía and upper Rio Negro basin.

Tococa cordata Berg ex Triana, Trans. Linnean Soc. Bot., 28:133. 1871. TYPE: VENEZUELA. Amazonas: Prope San Carlos ad Río Negro in Venezuela australi, *Spruce 3477* (lectotype: K [designated by Michelangeli (2001)]; isolectotypes: BR, K, NY, P).

Shrub; leaves cordate, domatia completely impressed in the leaf blade; inflorescences with caducus large bracts; flowers 5-merous; anthers blue to purple.

Colombia, Venezuela, Brazil, usually on the upper part of river banks, 50–200 m.

Tococa coronata Benth., J. Bot. (Hooker), 2:303. 1840. TYPE: BRITISH GUIANA [now GUYANA]: *Schomburgk 980 p. p.*, (holotype: G [photos at F, NY]; isotypes: BM [annotated by Wurdack as a isotype, but no collector information available], K, [3, one marked as holotype], NY, P[2]).

Tococa truncata Benth., J. Bot. (Hooker), 2:304. 1840. TYPE: BRITISH GUIANA [now GUYANA]: *Schomburgk 980 p. p.*, (holotype: K [photo at F]; isotypes: BM, BR, P, B-2, destroyed [photos at NY, F]).

Tococa egensis Naudin, Ann Sci. Nat. Bot., sér. 3, 16:92. 1851. TYPE: BRAZIL. Amazonas: in Brasilia septentrionali, prope urbiculam Ega (now Tefé), *Poeppig 17202*. (holotype: B, destroyed [photo at NY, F]; lectotype: P, designated by Michelangeli [2001]).

FIGURE 6. A. *Tococa spadiciflora*, inflorescence and leaves with petiolar domatia; B. *Tococa capitata* inflorescence and leaf with laminar domatia; C. *Tococa macrophysca* inflorescence and leaves with petiolar domatia; D. *Tococa guianensis* terminal branch with petiolar domatia; E. *Tococa guianensis*, longitudinal section of a domatium showing *Azteca* ant workers and eggs; F. *Tococa rotundifolia*, flowering branch. (photos: A, John Clark; B-E, Fabián A. Michelangeli).

Tococa longisepala Cogn., in Mart., Fl. Bras., 14(4):449. 1888. TYPE: BRAZIL: Alto Amazonas, prope Panure ad Rio Uaupes, *Spruce 2446* (lectotype: P designated by Michelangeli (2001); isolectotypes: P [2], K, BR [fragment]).

Tococa traillii Cogn., in Mart., Fl. Bras., 14(4):626. 1888. TYPE: BRAZIL: Alto Amazonas, as Sao Braz secus Purus, Mar 1875, *Trail 287* (holotype: K [photo F]; isotypes: BR, P [photo at F, NY]).

Tococa setifera Pilg., Verh. Bot. Ver. Brand., 47:177. 1905. TYPE: PERU. Amazonas: Jarua, Dec 1900, *Ule 5095* (holotype: B, destroyed [photo at F 16-2]).

Tococa glandulosa Gleason, Bull. Torrey Bot. Club, 53:252. 1931. TYPE: PERU, Loreto: Mishuyacu, near Iquitos, 100 m, Oct–Nov, 1929, *Klug 424*, (holotype: NY [Photo at BM]; isotype: US).

Shrubs; leaves lanceolate to elliptic, domatia immersed on the leaf blade, occasionally with the base projecting ⅓ into the apex of the petiole; flowers 5-merous, petals pink; anthers and fruits blue to purple.

Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia, riparian and seasonally flooded forests, 50–200 m.

Tococa costoides Michelangeli, Brittonia 58: 153. 2006. TYPE. BRAZIL. Amazonas: Caruari, Poço Juruá, Mata de terra firme, solo argiloso, 9 Jul 1980, *A. S. L. da Silva, N. A. Rosa & R. P. Bahia 575* (holotype: MG; isotype: US)

Trees or treelet up to 3.5 m; stem densely pubescent, the simple trichomes up to 4 mm long; leaves isophyllous to slightly anisophyllous, up to 29 cm long; domatia at the apex of the petiole, 1.2-2.2 cm long, ovoid; inflorescence and dichasia subtended by persistent bracts 2-3.5 x 2.5-4 cm; flowers, 5-merous, only partially visible at anthesis between the bracts.

Brazil, primary forests, 250-300 m.

Tococa filiformis (Gleason) Wurdack. Phytologia, 9:424. 1964. *Myrmidone filiformis* Gleason. Bull. Torrey Bot. Club, 57:74. 1930. TYPE: COLOMBIA. Caquetá: between Santa Marta and Marsella, 4 Aug 1926, *Woronow & Juzepczuck 6421* (holotype: L [n. v.], photo at US).

Shrubs; stems hirsute; the trichomes 6–9(–12) mm long, with flattened bases; leaves slightly dimorphic, with domatia on the larger leaves only; domatia at the apex of the petiole; inflorescence terminal; flowers 6-merous, outer calyx filiform, up to 16 mm long.

Colombia, known only from the Caquetá basin, 400–800 m.

Tococa gonoptera Gleason, Bull. Torrey Bot. Club, 58:247.1931. TYPE: PERU. Loreto: between Yurimaguas and Balsapuerto, lower Río Huallaga basin, 26–31 Aug 1929, *Killip & Smith 28902* (holotype: NY; isotypes: F, K, US).

Shrubs; stems quadrangular when young, becoming terete; leaves isomorphic to slightly dimorphic, 5-nerved; domatia at the apex of the petiole, free from the blade, 1–2 cm long; flowers 5-merous, the hypanthium with 10 wings that run from the base of the hypanthium to the torus, one set larger and opposite the calyx; petals pink.

Peru, primary forests, 130–1000 m.

Tococa guianensis Aubl., Hist. Pl. Guiane, 1:437, pl 174. 1775. *Melastoma physophora* Vahl, Eclog. Amer. 1:45. 1797. *Melastoma tococo* Desr., Lam., Encycl. 4: 39. 1797. TYPE: FRENCH GUIANA: ad margines viarum Caiennae & Guianae, *Aublet s. n.* (holotype: BM; isotypes: P[2]).

Tococa guianensis var. *orinocensis* Wurdack. Mem. New York Bot. Gard., 10:175. 1964. TYPE: VENEZUELA. Amazonas: sabana Huachapana, Río Orinoco, 30 km above Santa Barbara, 125 m, 15 Sep 1957, *Maguire, Wurdack & Keith 41468* (holotype: US; isotypes: K, NY, P, VEN).

Tococa guianensis var. *macrophysca* Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:89. 1851. Type: FRENCH GUIANA: *Poiteau s. n.* (syntype: P; isosyntype: P); *1821, Perrotet, s.n.* (syntype: P); *Bonpland s.n.* (syntype: P)

Tococa aubletii D. Don, Mem. Wernerian Nat. Hist. Soc., 4:304. 1823. Type: Locality, collector and date unknown. (LINN).

Tococa formicaria Mart. ex DC., Prodr., 3:165. 1828. Type: BRAZIL. Goyaz: sylvis profundis, *Mart. 6333* (holotype: M [photos at F, NY]).

Tococa vesiculosa DC., Prodr., 3:166. 1828. Type: Mexico, *Sesse & Mocino* (copy of drawing).

Tococa barbata Benth., J. Bot. (Hooker), 2:305. 1840. Type: BRITISH GUIANA [now GUYANA]: Pedrero, *Schomburgk 887* (holotype: K; isotypes: BM, K, NY, P-3). = *Tococa guianensis.*

Tococa roreimi Hook., J. Bot., 2:305. 1840. Type: BRITISH GUIANA [now GUYANA]: Mount Roraima, *Schomburgk s. n.* (holotype: K).

Tococa cachimbensis Brade, Arquiv. Jard. Bot. Rio de Janeiro, 16:14. 1959. Type: BRAZIL. Para: Serra do Cachimbo, 15 Nov 1955, *E. Pereira 1796* (holotype: RIO [Photo F]).

Tococa acuminata Benth, Bot. Voy. Sulph., 94. 1844. Type: COLOMBIA: Isle of Gorgona, *Sinclair s. n.* (holotype: K [photo at F, Negative 93-12]).

Tococa cardiophylla Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:93. 1851. Type: BRAZIL. Bahia: in Brasilia septentrionali prope Bahiam, *Blanchet s. n* (holotype: P; isotype: G[n. v.]).

Tococa didymophysca Naudin, Ann. Sci. Nat. Bot., sér. 3, 16: 90. 1851. *Tococa formicaria* var *didymophysca* (Naudin) Cogniaux. in Mart., Fl. Bras. 14(4):440. 1888. Type: BRAZIL. Minas Gerais: *Claussen 603* (holotype: P; isotypes: K, P).

Tococa latifolia Naudin, Ann. Sci. Nat. Bot., sér. 3, 16: 90. 1851. BRAZIL: locality and date unknown, *A. R. Ferreira, s.n.* (holotype: P [photos at F, NY]; isotype: P[2]).

Tococa occidentalis Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:92. 1851. Type: PERU: locality and date unknown, *Mathews 1306* (holotype: K [photo at F 92-2]; isotypes: BM, P[2], [one marked as holotype]).

Tococa coriaceae S. Moore, J. Bot., 18:3. 1880. Type: BELIZE: unde misit prefectus Barlee. (holotype: K [photo at F 95-10]).

Tococa formicaria var. *gardneri* Cogn., in Mart., Fl. Bras., 14(4):440. 1888. Type: BRAZIL. Goyaz: 1841, *Gardner 3741* (holotype: NY; isotypes: BM, K[2], NY[2], P).

Tococa platyphysca Cogn., in Mart., Fl. Bras., 14(4):437. 1888. Type: BRAZIL. Alto Amazonas: Ega, sylvis densa, *Poeppig 2571* (holotype: B [destroyed]; isotypes: BR[2], P, W [photo at F]).

Tococa subglabrata Cogn., in Mart., Fl. Bras., 14(4):438. 1888. Type: BRAZIL: Piauhy, *Gardner 2862* (lectotype: P, designated by Michelangeli (2001); isolectotypes: BR, BM, G n. v., K[2], NY, P[2]).

Tococa discolor Pilg., Verh. Bot. Ver. Brand., 47: 176. 1905. Type: BRAZIL: Jurua Miry [*sic*], Puritisal, auf terra firme, Jun 1901, *Ule 5553*. (holotype: B, destroyed [photos at F Neg. 15-11, NY]).

Tococa juruensis Pilg., Verh. Bot. Ver. Brand., 47: 176. 1905. Type: BRAZIL. Amazonas: Unterer Jarua, Fortaleza, *Ule 5914* (holotype, B, destroyed [photo NY]; lectotype: K designated by Michelangeli [2001]).

Tococa peckiana B. L. Robinson, Proc. Amer. Acad. Arts, 45:395. 1910. Type: BRITISH HONDURAS [now BELIZE]: in thickets near Manatee Lagoon, *Peck 68* (holotype: GH; isotypes: G, K, NY).

Tococa loretensis Ule, Notizbl. Bot. Gart. Berlin-Dahlem, 6:365. 1915. Type: PERU. Loreto: Iquitos, Jul 1902, *Ule 6234* (holotype: B, destroyed [photo at F, 16-1, fragment attached]).

Maieta glandulifera Standl., Proc. Biol. Soc. Wash., 37:52. 1924. TYPE: GUATEMALA: swamp at Puerto Barrios, 0 m, Jun 1922, *Standley 25002* (holotype: US).

Tococa chuivensis Wurdack, Phytologia, 9:423. 1964. TYPE: PERU. Amazonas: Bagua, rainforest in quebrada Chiuvi, km 278 of Marañon Road, 500–550 m, 10 Sep 1962, *Wurdack 1920* (holotype: US; isotypes: F, K, NY, SM).

Tococa mexiae Wurdack, Phytologia, 9:422. 1964. TYPE: PERU. Amazonas: Bagua, forested ridge along Río Santiago 2–3 km above mouth, 300–350 m, 25 Oct 1962, *Wurdack 2406* (holotype: US; isotypes: F, K, NY, USM).

Tococa chivuensis var. *ecuadorensis* Wurdack, Phytologia, 26:399. 1973. TYPE: ECUADOR. Pastaza: between Veracruz and Cabeceras 20 Jan 1971, *Lugo 1334* (holotype: GB; isotypes: F, NY, US).

Shrubs to small trees; domatia free from the leaf blade; flowers 5-merous, petals pink; ovary with an apical corona of short setae; mature fruits black. Figs. 2E, 6D–E.

Mexico, Guatemala Nicaragua, Costa Rica, Panamá, Colombia, Venezuela, Guyana, French Guiana, Suriname, Ecuador, Peru, Brazil, Bolivia, widespread in the Amazon and Orinoco basins from 50–1500 m, rarer in Central America, 50–400 m.

Extremely variable and widespread species, with many ecologycal variants. See Michelangeli (2005) for a discussion on specific limits and relationships to other myrmecophitic *Tococa*.

The type of *Tococa latifolia* was incorrectly cited as *Bonpland 36324* by Michelangeli (2005); according to Wurdack (1971), the type is a collection from A. R. Ferreira from Brazil.

Tococa hirta Berg ex Triana, Trans. Linnean Soc., Bot., 28:132. 1871. TYPE: VENEZUELA. Amazonas: San Carlos de Río Negro, *Spruce 3145* (lectotype: K, designated by Michelangeli (2001); isolectotypes: BR, P).

Shrub; domatia ¼–⅓ immersed in the leaf blade; inflorescences psudoaxillary and terminal on the same individual, subtended by a caducus sheathing bract; flowers 5-merous, petals white.

Colombia and Venezuela, 100–200 m, rarely collected species in the Guainia and upper Río Negro basin.

Tococa lancifolia Spruce ex Triana, Trans. Linnean Soc., Bot., 28:133. 1871. TYPE: VENEZUELA. Amazonas: ad flumina Casiquiari, Vasiva et Pacimoni, *Spruce 3313* (holotype: K; isotypes: BR, K, G, GOET [n.v.] NY, P-3).

****Tococa lancifolia** var. **anaphysca** Wurdack, Phytologia, 52 (1):67. 1982. TYPE: VENEZUELA. Amazonas: Río Atacavi, cerca Río Atabapo, 100 m, 10–24 Nov 1980, *Piñate & Mondolfi 1034* (holotype: US; isotypes: NY, K).

Shrubs; leaves lanceolate, the domatia immersed in the leaf base; flowers 5-merous; anthers and fruits blue to purple.

Venezuela, seasonally flooded forests, especially along black-water streams or rivers, 50–200 m.

Tococa leticiana Michelangeli, Brittonia 58: 151. 2006. TYPE: COLOMBIA. Amazonas: Municipio Leticia, 8-20 km carretera Leticia-Tarapacá, orilla del bosque y bosque primario perturbado, 69°57′W, 4°03′S, 300 m, 27 Sep. 1991, *J. Betancur, B. Echeverry, J. Kress & Ch. Roesel 2820* (holotype: COL; isotypes: HUA, NY, US).

Trees up to 10 m; stems densely pubescent, the trichomes eglandular up to 5 mm long; leaves isomorphic up 17-50 cm long with domatia 1.5-2.5 cm, ovoid, at the apex of the petiole; inflorescences subtend by bracts 7.5-11 x 3.5-6 cm, caducous, surrounding the developing inflorescence, sub-orbicular to elliptic with an acuminate apex 2-4 cm long, the abaxial surface red; flowers 5 merous.

Colombia. forests. 300 m.

Tococa macrophysca Spruce ex Triana, Trans. Linnean Soc., Bot., 28:132. 1871. TYPE: COLOMBIA: near Panure at Río Uaupes and S. Gabriel of Río Negro, *Spruce 2188* (lectotype: K, designated by Michelangeli (2001); isolectotypes: P, BR [fragment], V [n.v.]).

Maieta robusta Rusby, Descr. S. Am. Pl. 72:1920. TYPE: BRAZIL. Amazonas: Rio Negro, 1907–1908, *Weiss s.n.* (holotype: NY; isotype: NY).

Shrubs to small trees; domatia free from the leaf blade, smooth, with apical ascending lobes; inflorescences pseudo-lateral cymes; flowers 5-merous, petals white. Figs. 2F, 6C.

Venezuela, Colombia, Brazil, non-flooded forests 100–300 m.

Tococa macroptera Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:94. 1851. TYPE: BRAZIL. Goyaz: *Gardner 3174* (lectotype: P, designated by Michelangeli (2001); isolectotypes: BM, K[3], NY, P[2]).

Tococa macedoi Brade, Arquiv. Jard. Bot. Río de Janeiro, 16:32. 1959. TYPE: BRAZIL. Minas Gerais: Filadelfia, 10 Oct 1955, *Macedo 4021* (holotype: MG; isotypes: K[2], US).

Shrubs; leaves 5-nerved, apex caudate, dimorphic, the smaller ones reduced 30–50%, domatia globose to ovoid, up to 4 cm long, present always in the larger leaves, occasionally in the smaller ones; flowers 5-merous, the hypanthium with 5 ribs opposite the calyx, petals pink.

Brazil, in forests up to 500 m.

Tococa macrosperma Mart., Nov. Gen. Sp. Pl., 3:148, pl. 279. 1832. *Myrmidone macrosperma* (Mart.) Mart., Nov. Gen. Sp., 3: 149. 1832. TYPE: BRAZIL: *Martius s.n.* (holotype: G).

Myrmidone lanceolata Cogn., in Mart., Fl. Bras., 14(4):468, pl. 98, fig 2. 1888. TYPE: BRAZIL. Alto Amazonas: Río Negro, prope San Gabriel de Cachoeira, *Spruce 2336* (lectotype: K [designated by Michelangeli 2005]; isotype: GH).

Hormocalyx hirsutus Gleason, Phytologia, 1:174. 1935. TYPE: BRAZIL. Amazonas: Humayta, on plateau between Río Livramento and Río Ipixuna, *Krukoff 7098* (holotype: NY; isotypes: BM, K).

Shrubs; leaves dimorphic, the larger one with domatia at the base of the leaf blade, base cordate; flowers 6-merous, the outer calyx connate and forming a "skirt" around the hypanthium; petals initially red, turning white after anthesis. Fig. 5F.

Colombia, Venezuela, Guyana, Peru, Brazil, Bolivia, primary forests 100–1300 m.

Tococa obovata Gleason, Bull. Torrey Bot. Club, 58:429. 1931. TYPE: VENEZUELA. Amazonas: Mount Duida, 1450 m, 5 Jan 1929, *Tate 593* (holotype: NY).

****Tococa obovata** subsp. **obovata**

Tococa montana Gleason, Bull. Torrey Bot. Club, 58:430. 1931. TYPE: VENEZUELA. Amazonas: Summit of Mount Duida, 1350 m, 1–4 Jan 1929, *Tate 1009* (holotype: NY; isotype: K).

***Tococa obovata** subsp. **neblinensis** Wurdack, Mem. New York Bot. Gard., 10:175. 1964. TYPE: VENEZUELA. Amazonas: Cerro la Neblina, 1800 m, 12 Nov 1957, *Maguire, Wurdack & Maguire 42055* (holotype: US; isotypes: K, NY, VEN).

Shrubs; leaves foveolate (in the myrmecophitic subspecies), the domatia completely immersed in the leaf base (if present); flowers 5-merous, petals dark pink to red.

Endemic to Cerro La Neblina in Venezuela, 1800–2400 m.

Tococa pachystachya Wurdack, Mem. New York Bot. Gard., 10:43, fig 33C–G. 1961. TYPE: VENEZUELA. Amazonas: Cerro La Neblina, 1600 m, 24 Jan 1954, *Maguire, Wurdack & Buntig 37368* (holotype: NY; isotypes: F, K, US, VEN).

Shrubs; domatia ⅔ to totally impressed in the leaf blade, with short and thick trichomes; inflorescences with a thickened peduncle and sessile flowers; flowers 5-merous.

Venezuela, Brazil, tepui summit and slope forests, 1400–2100 m.

Tococa parviflora Spruce ex Triana, Trans. Linnean Soc., Bot., 28:132. 1871. TYPE: PERU: Tarapoto, Río Mayo, Jul–Aug 1856, *Spruce 4617* (holotype: K; isotypes: B [destroyed, photos F, NY), BM, BR[2], K[2], P).

Tococa parviflora var. *mansenrichensis* Wurdack, Phytologia, 9:424. 1964. TYPE: PERU. Loreto: Alto Amazonas, Río Marañon, near Teniente Pinglo, just above Pongo de Manseriche, 250–300 m, 4–7 Oct 1962, *Wurdack 2092* (holotype: US; isotypes: F, K, NY, USM).

Tococa tetramera Wurdack, Phytologia, 24: 204.1972. TYPE: PERU. San Martín: Mariscal Caceres, Nuevo Progreso, Río Huallaga, Uchiza, 500 m, 18 Jun 1969, *Schunke 3151* (holotype: US; isotype: F).

Shrubs; leaves slightly dimorphic, domatia at the apex of the petiole, usually on both leaves of each pair; inflorescence a terminal panicle; flowers 4-merous, anthers white to yellow, with an orbicular gland on the dorsal portion of the connective.

Colombia, Ecuador, Peru, Brazil, and a disjunct population in Venezuela, understory of primary forests 200–1000 m.

Tococa pauciflora Spruce ex Triana, Trans. Linnean Soc., Bot., 28:131. 1871. TYPE: VENEZUELA. Amazonas: Río Guainía, above mouth of Río Casiquiare, *Spruce 3522* (holotype: K; isotypes: BM, BR, NY, P).

Shrubs to small trees; leaves lanceolate to oblong, domatia free from the leaf, to 4 cm long; flowers 5-merous, calyx with 5 wings opposite the calyx, outer teeth projecting vertically.

Colombia, Venezuela, 50–200 m.

Tococa quadrialata (Naudin) J.F. Macbr., Publ. Field. Mus. Nat. Hist., Bot. Ser., 13: 474. 1941. *Microphysa quadrialata* Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:99. 18 tab. 3, fig II. 1851. *Microphysca quadrialata* (Naudin) Naudin, Ann. Sci. Nat. Bot., sér. 3, 18: 292. 1852. TYPE: PERU: Cuzco, *Gay s. n.* (holotype: P).

Shrubs; stems quadrangular when young, becoming terete; leaves dimorphic, the smaller one up to 30% reduced, 5-nerved; domatia at the apex of the petiole, free from the blade, 1–2 cm long; flowers 4-merous, the hypanthium with 8 wings that run from the base of the hypanthium to the torus, one set larger and opposite the calyx; petals pink.

Peru, primary forests, 130–1400 m.

Tococa racemifera Wurdack, Phytologia, 48:247. 1981. TYPE: COLOMBIA. Antioquia: wet forest, 3 km from Planta Providencia, 28 Km SW of Zaragoza, Río Anori Valley, 400–700 m, 21 Feb 1977, *Alverson, White & Shepherd 66* (holotype: US; isotypes: NY [2], WIS[n.v.]).

Shurbs; leaves dimorphic, the larger smaller one reduced up to 80%; domatia present in the larger leaf only, 1.4–1.7 cm long, at the apex of the petiole, free from the leaf blade or slightly immersed; inflorescences slender unbranched racemes up to 26 cm long, terminal, but becoming lateral by growth of the lateral meristem; flower sessile, 5-merous, petals white.

Colombia, montane forest in Antioquia, up to 1300 m.

Tococa rotundifolia (Triana) Wurdack, Phytologia, 19:193. 1969. *Microphysca rotundifolia* Triana, Trans. Linnean Soc., Bot., 28: 141. 1871. TYPE: VENEZUELA. Amazonas: in forests at San Carlos de Río Negro, Oct, *Spruce 3130* (holotype: K; isotypes: BM, P[2]).

Small shrubs; domatia immersed in the leaf blade; flowers 5-merous, hypanthium red, with the calyx outer teeth projecting downward forming 5 wings, petals red. Fig. 6F.

Colombia, Venezuela, Brazil, in white sand soils, 100–300 m.

Tococa spadiciflora Triana, Trans. Linnean Soc., Bot., 28:132. 1871. TYPE: COLOMBIA. Chocó: *Triana 4104* (holotype: K, isotypes: P, COL).

Shrubs; leaves isomorphic, 5(–7)-nerved, the domatia free from the leaf blade, 1.3–2.2 cm long, deeply corrugated and with large pores throughout the surface; inflorescences terminal, racemose, 6–15(–18) cm long; flowers sessile, 5-merous, petals green, emaginate. Figs. 2G, 6A.

Colombia, Ecuador, primary and secondary forest understory, up to 1000 m.

The type was incorrectly cited as *Triana 36327* by Michelangeli *(*2005). Leaves and domatia are similar to *Clidemia killipii* but are differentiated by the inflorescence architecture and position, as well as overall flower morphology.

Tococa stellata Gleason, Bull Torrey Bot. Club, 57:73. 1930. TYPE: COLOMBIA. Caquetá: Corea, near Hetucha, 20 Jul 1926, *Woronow 6053* (holotype: LEN [n.v.]).

Shrubs; stems terete; leaves dimorphic, the larger one with domatia up to 2.5 cm long, the smaller one with domatia up to 0.5 cm long or lacking domatia; flowers 5-merous, the hypanthium conical and with 10 densely glandular-setose wings running from the base to the torus, of two different sizes, the larger ones projecting up to 1.5 mm from the surface of the hypanthium and opposite the calyx, pubescent with a mix of glandular and non-gladular trichomes.

Colombia, known only from the type.

Tococa stenoptera Gleason, Bull. Torrey Bot. Club, 58:248. 1931. TYPE: PERU. Junín: Puerto Yessup, 400 m, 10–12 Jul 1929, *Killip & Smith 26280* (holotype: NY; isotypes: F, US).

Shrubs to small trees; stems sparsely glandular setose, the tricomes up to 2 mm long; leaves dimorphic, the larger ones 13–22(–28) long, the smaller ones close to 50% reduced; domatia 2–3 cm long, globose to ovoid, at the apex of the petiole, free from the leaf blade, usually present only in the larger leaves, occasionally in both leaves; inflorescences terminal, paniculate, 8–15 cm long; flowers 5-merous, hypanthium conical with 5 wings opposite the calyx, 0.5 mm wide running the length of the hypanthium, anthers yellow, stigma peltate.

Ecuador, Peru, Amazonian forest, up to 300 m.

Tococa stephanotricha Naudin, Ann. Sci. Nat. Bot., sér. 3, 16:95. 1851. TYPE: BRAZIL. Amazonas: in Brasilia septentrionali, secus flumen Amazonum, loco dicto Maynas Alto, *Poeppig 1844* (holotype: P; isotype: BR).

Tococa temnoptera Gleason, Bull. Torrey Bot. Club. 58:249. 1931. TYPE: PERU. Junín: Puerto Yessup, 400 m, 10–12 Jul 1929, *Killip & Smith 26237* (holotype: NY; isotypes: F, K US).

Shrubs to 3(–4.5) m; stems terete, densely glandular-setose, the tricomes 3–4 mm long; leaves 5-nerved, slightly dimorphic, the smaller one 20–25% reduced; domatia at the apex of the petiole, free from the leave blade, globose to ovoid, 0.8–1.5(–2.5) cm long; inflorescences terminal or axillary, 3–7(–10) cm long, paniculate; flowers 4–5-merous, the hypanthium conical and with 8–10 densely glandular-setose wings running from the base to the torus, of two different sizes, the larger ones projecting up to 1.5 mm from the surface of the hypanthium and opposite the calyx, pubescent with a mix of glandular and non-gladular trichomes; petals red to dark pink; stigma peltate.

Colombia, Peru and Brazil, in lowland and montane forests, from 200–1100 m.

Tococa symphyandra (Triana) Cogn. DC., Mon. Phan., 7:963. 1891. *Miconia symphyandra* Triana, Trans. Linn. Soc. Bot. 28:126. 1871. TYPE: COLOMBIA: Barbacoas, 1600 m, 1853, *Triana 4102* (holotype: K; isotypes: BM, BR, COL, P).

Miconia barbicaulis Gleason, Bull. Torrey Bot. Club, 68: 248. 1941. TYPE: ECUADOR. Pastaza: Puyo, 750–1000 m, Aug 1939, *Skutch 4420* (holotype: NY; isotype: US [fragment]).

Tococa variegata Markgraf, Notizbl. 15:379. 1941. TYPE: ECUADOR. Pastaza: Mera, 7 Sep 1938, 1000 m, *Schultze & Rhonhof 2786* (holotype: B[destroyed]).

Shrubs; stems pubescent, the trichomes 5–15 mm long, retrorse; leaves isomorphic or nearly so, broadly ovate to cordate, 7(–9)-nerved if domatia absent, plinerved if domatia present immersed at the base of the leaf blade; domatia when present, 1.2–2.2 × 0.8–1.2 cm; inflorescences terminal, paniculate, 8–20 cm long; flowers 5-merous, anthers yellow, laterally connivent, forming a ring around the style, the connective base prolonged into a triangular appendage.

Colombia, Ecuador, understory of montane and cloud forests, up to 2000 m.

Tococa undabunda J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 4:177. 1929. TYPE: PERU. Junín: La Merced, Hacienda Schunke, 27 Aug–1 Sep 1923, *Macbride 5734* (holotype: F; isotype: K).

Shrub; domatia at the apex of the petiole, fusiform, the ⅓–⅕ apex immersed in the leaf blade; inflorescences capitate, bracteoles absent; flowers 5-merous.

Peru, known only from the type.

TOPOBEA: aprox. 70 species, 3 myrmecophites. *Topobea* is closely related to *Blakea* and most likely not monophyletic (Penneys et al. 2004a). All three species of myrmecophitic *Topobea* have hollow stems.

Topobea gracilis Triana, Trans. Linnean Soc., 28:150. 1871. TYPE: COLOMBIA: Barbacoas ad alt 900 ped, *Triana, 4085* (holotype: P).

Hemiepiphyte; primary domatia in hollow swollen twigs; leaves 5-nerved; flowers 6-merous.

Colombia, 50–1000 m.

Topobea inflata Triana, Trans. Linnean Soc., 28:150. 1871. TYPE: COLOMBIA: inter Barbacoas et Tuquerres Novae Granatae ad alt. 2100 ped., 1851–57, *Triana 4055*, (holotype: P).

Hemiepiphyte; primary domatia in hollow swollen twigs; leaves 3-nerved; flowers 6-merous. Fig. 1B.

Colombia, 100–1000 m.

Topobea pluvialis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., 22:162. 1940. TYPE: PANAMÁ. Darién: Chepigana District, crest of Cana-Cusai trail, 1200 m, 15 Mar 1940, *M. E. & R. A. Terry 1560* (holotype: F; isotype: MO).

Hemiepiphyte; primary domatia in hollow swollen twigs; leaves plinerved with mite domatia on the abaxial surface; flowers 6-merous.

Panamá, 900–1650 m.

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Appendix

SYNONYMS

The following is a list of both homotypic (≡) and heterotypic synonyms (=). Heterotypic synonyms are based on previous usage or monographs. No new synonyms are proposed in this annotated list. Type specimen information and description citations are given with the currently accepted name.

Calophysa dentata ≡ *Clidemia sprucei*
Calophysa heterophylla ≡ *Clidemia heterophylla*
Calophysa setosa ≡ *Clidemia setosa*
Calophysa tococoidea ≡ *Clidemia tococoidea*
Clidemia impetiolaris = *Clidemia pilosa*
Clidemia trichogona = *Clidemia setosa*
Conostegia hispida = *Conostegia dentata*
Cryptophysa setosa = *Conostegia setosa*
Hormocalyx hirsutus = *Tococa macrosperma*
Leandra bullifera ≡ *Ossaea bullifera*
Maieta cuneata ≡ *Henriettella cuneata*
Maieta dentata ≡ *Clidemia sprucei*
Maieta glandulifera = *Tococa guianensis*
Maieta guianensis var. *leticiana* = *Maieta guianensis*
Maieta guianensis var. *peruviana* = *Maieta guianensis*
Maieta heterophylla ≡ *Clidemia heterophylla*
Maieta hispida = *Maieta guianensis*
Maieta hypophysca = *Maieta guianensis*
Maieta juruensis ≡ *Clidemia juruensis*
Maieta robusta = *Tococa macrophysca*
Maieta setosa ≡ *Clidemia setosa*
Maieta tococoidea ≡ *Clidemia tococoidea*
Maieta tococoidea var. *watsonii* = *Clidemia crenulata*
Majeta dispar = *Maieta guianensis*
Melastoma heterophylla ≡ *Clidemia heterophylla*
Melastoma mayeta Willd. ≡ *Maieta guianensis*
Melastoma physophora ≡ *Tococa guianensis*
Melastoma tococo ≡ *Tococa guianensis*
Miconia barbicaulis = *Tococa symphyandra*
Miconia symphyandra ≡ *Tococa symphyandra*
Microphysa quadrialata ≡ *Tococa quadrialata*
Microphysca quadrialata ≡ *Tococa quadrialata*
Microphysca rotundifolia ≡ *Tococa rotundifolia*
Myrmidone filiformis ≡ *Tococa filiformis*
Myrmidone lanceolata = *Tococa macrosperma*
Myrmidone macrosperma ≡ *Tococa macrosperma*
Pterocladon sprucei ≡ *Miconia baillouiana*
Staphidiastrum impetiolare = *Clidemia pilosa*
Tococa acuminata = *Tococa guianensis*
Tococa aubletii = *Tococa guianensis*
Tococa barbata = *Tococa guianensis*
Tococa bullifera var. *glabrata* = *Tococa bullifera*
Tococa bullifera var. *leiocalyx* = *Tococa bullifera*
Tococa cachimbensis = *Tococa guianensis*
Tococa cardiophylla = *Tococa guianensis*
Tococa chivuensis var. *ecuadorensis* = *Tococa guianensis*
Tococa chuivensis = *Tococa guianensis*
Tococa coriaceae = *Tococa guianensis*
Tococa didymophysca = *Tococa guianensis*
Tococa discolor = *Tococa guianensis*
Tococa egensis = *Tococa coronata*
Tococa formicaria = *Tococa guianensis*
Tococa formicaria var. *gardneri* = *Tococa guianensis*
Tococa glandulosa = *Tococa coronata*
Tococa guianensis var. *macrophysca* = *Tococa guianensis*
Tococa guianensis var. *orinocensis* = *Tococa guianensis*
Tococa juruensis = *Tococa guianensis*
Tococa lancifolia var. *anaphysca* = *Tococa lancifolia*
Tococa latifolia = *Tococa guianensis*
Tococa longisepala = *Tococa coronata*
Tococa loretensis = *Tococa guianensis*
Tococa macedoi = *Tococa macroptera*
Tococa mayeta ≡ *Maieta guianensis*
Tococa mexiae = *Tococa guianensis*
Tococa micrantha = *Tococa caquetana*
Tococa occidentalis Naudin = *Tococa guianensis*
Tococa parviflora var. *mansenrichensis* = *Tococa parviflora*
Tococa peckiana = *Tococa guianensis*
Tococa platyphysca = *Tococa guianensis*
Tococa roreimi = *Tococa guianensis*
Tococa setifera = *Tococa coronata*
Tococa spruceana = *Tococa bullifera*
Tococa subglabrata = *Tococa guianensis*
Tococa temnoptera = *Tococa stephanotricha*
Tococa tetramera = *Tococa parviflora*
Tococa traillii = *Tococa coronata*
Tococa truncata = *Tococa coronata*
Tococa ulei Pilg. = *Tococa bullifera*
Tococa variegata = *Tococa symphyandra*
Tococa vesiculosa = *Tococa guianensis*
Topobea punctulata ≡ *Blakea punctulata*

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Phylogenetic Revision of *Xylosandrus* Reitter (Coleoptera: Curculionidae: Scolytinae: Xyleborina)

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A phylogenetic revision of the xyleborine genus *Xylosandrus* Reitter based on morphological and molecular data sets is presented. The monophyly of the genus was tested using a 43 character morphological data set analyzed separately and in combination with a molecular data set comprised of five independent gene loci: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear protein-coding genes arginine kinase (ArgK), CAD (rudimentary), and elongation factor 1-α (EF-1α). *Xylosandrus* was recovered as polyphyletic with the present classification containing species from four other genera: *Amasa* Lea, *Anisandrus* Ferrari, *Cnestus* Sampson, *Euwallacea* Hopkins, as well as *Xylosandrus*. A taxonomic revision of *Xylosandrus* is presented based on these results. The following new combinations are given: *Amasa cylindrotomicus* (Schedl), *A. omissus* (Schedl), *A. oralis* (Schedl), *Anisandrus butamali* (Beeson), *A. ursa* (Eggers), *A. ursinus* (Hagedorn), *A. ursulus* (Eggers), *Cnestus ater* (Eggers), *C. fijianus* (Schedl), *C. gravidus* (Blandford), *C. improcerus* (Sampson), *C. laticeps* (Wood), *C. mutilatus* (Blandford), *C. orbiculatus* (Schedl), *C. peruanus* (Wood), *C. retifer* (Wood), *C. retusus* (Eichhoff), *C. testudo* (Eggers), *Cyclorhipidion squamulatum* (Beaver and Löyttyniemi) all listed in *Xylosandrus* by Wood and Bright (1992); *Xylosandrus amputatus* (Blandford) and *X. mixtus* (Schedl) are transferred from *Amasa*, *X. russulus* (Schedel) from *Euwallacea*, and *X. rotundicollis* (Browne) from *Xyleborus* Eichhoff. Two new species of *Xylosandrus* are described: *X. borneensis* and *X. hulcri*. An illustrated key to species of *Xylosandrus* worldwide is provided.

KEYWORDS: Biogeography, host plants, diagnosis, and images are presented for each species.

The scolytine subtribe Xyleborina contains approximately 1,300 described species and constitutes one of the largest radiations of ambrosia beetles (Wood and Bright 1992; Jordal 2002). The xyleborine mating system, which includes haplodiploidy and extreme inbreeding, is believed to be the cause of this dramatic radiation (Normark et al. 1999). Xyleborina are absent from the Dominican amber fossil record, suggesting that their radiation began in the Miocene (Bright and Poinar 1994; Jordal et al. 2000). Ambrosia beetles bore into the xylem of host trees and feed on symbiotic fungus, which grows on the walls of their galleries. This ambrosial feeding habit has evolved multiple times within the Scolytinae and also in the related weevil subfamily Platypodinae (Jordal et al. 2000; Farrell et al. 2001). Ambrosia beetles tend to be less host-specific than their bark beetle counterparts because adaptation to host secondary chemistry has not likely influenced their radiation (Beaver 1979). This lack of host specificity, along with their haplodiploidy mating system and inbreeding, make Xyleborina beetles particularly suited for the invasion of new habitats and establishment as introduced exotic species (Haack 2006; Rabaglia et al. 2006). In theory, a single female beetle could establish an invasive population of beetles. Furthermore, low host specificity means that invasive beetles do not need to locate a specific host and can infest multiple species. The economic importance of invasive xyleborines, along with their interesting biology and ecology, has prompted much research interest in the subtribe. Recently, the classification of the Xyleborina has been studied within a phylogenetic context to update their classification within an evolutionary framework (Jordal et al. 2000; Jordal 2002; Hulcr et al. 2007).

Xylosandrus Reitter (1913) is a large genus of xyleborine ambrosia beetles with a widespread distribution primarily in tropical but also in temperate regions throughout the world. In their worldwide catalog of the Scolytinae, Wood and Bright (1992) list 52 species of *Xylosandrus*. Subsequent descriptions, new synonymies, and new combinations have brought the present number to 54 species (Bright and Skidmore 1997, 2002; Saha et al. 1992; Wood 2007; Dole and Beaver 2008). Several *Xylosandrus* species cause economic losses in nursery and agricultural settings in their native and introduced ranges. In Brazil, *X. compactus* (Eichhoff) causes losses in several economically important host species, including avocado, cacao, coffee, and mango (Oliveira 2008). *Xylosandrus crassiusculus* (Motschulsky) may potentially impact native tropical fauna, as the species is present as an invasive in Costa Rican primary forests (Kirkendall and Ødegaard 2007). Five *Xylosandrus* species currently occur in North America and of these, only one is native, *X. curtulus* (Eichhoff). The other four, *X. compactus, X. germanus* (Blandford), *X. crassiusculus*, and *X. multilatus* (Blandford) have been introduced from the Old World tropics (Rabaglia 2002; Rabaglia et al. 2006). In North America, three *Xylosandrus* species (*X. compactus*, *X. crassiusculus*, and *X. germanus*) have caused "considerable economic damage" since their introductions (Oliver and Mannion 2001). It is difficult to get exact figures on the economic losses attributed to *Xylosandrus* species, since these numbers are often grouped with damage caused by other xyleborines. As an example, nursery managers in Maryland reported individual loses of $3,650–$8,400 in nursery stock to *Xylosandrus* species in the spring of 2008 alone (R. J. Rabaglia, pers. com.).

The current classification of *Xylosandrus* contains species with highly variable morphologies, several of which are similar to those of other xyleborine genera (Hulcr et al. 2007; Dole and Beaver 2008). Recent phylogenetic analyses of molecular data have also suggested that *Xylosandrus* is polyphyletic (Jordal 2002; Dole et al. 2010). Given the apparent taxonomic ambiguities and the economic importance of this group (Dole and Beaver 2008; Dole et al. 2010), a revised classification based on morphological and molecular evidence is needed. Furthermore, clear diagnostic characters and a key to worldwide species are necessary for the classification to be a predictive and useful tool in identification and control of invasive *Xylosandrus* species.

In this study, we define 43 morphological characters in an effort to resolve taxonomic ambiguities among *Xylosandrus* species and related genera. We conduct a combined phylogenetic analysis of these taxa using these morphological characters and molecular data in order to guide a revision of *Xylosandrus*.

SYSTEMATICS

Xylosandrus was established as a monotypic genus by Reitter in 1913, with the type species *Xyleborus morigerus* Blandford. The genus remained monotypic for many years until Hoffmann (1941) transferred *Xyleborus germanus* into *Xylosandrus*. Following this, Nunberg (1959) transferred *Xyleborus compactus* into *Xylosandrus* and scolytine taxonomists began to take notice of the genus. Schedl (1963a) disagreed with the designation of the genus and listed *Xylosandrus* as a synonym of *Xyleborus* Eichhoff. Browne (1963) noted character differences that he felt justified the genus, chiefly the "broad, obtuse prosternal process separating the front coxae," and transferred 14 species from *Xyleborus* to *Xylosandrus*. Schedl (1964) agreed with Browne's assessment and transferred 8 more species from *Xyleborus* to *Xylosandrus*. Later, Schedl (1971) for the first time described two species in *Xylosandrus*, rather than transferring them from *Xyleborus*: *X. adherescens* and *X. assequens*.

In 1982, Wood began transferring species into *Xylosandrus*, chiefly from *Xyleborus*, and within a decade the genus grew to include 52 species (Wood 1982, 1984; Wood and Bright 1992). At this point in its taxonomic history, the generic limits and defining characters of *Xylosandrus* were blurred. Many species transferred to *Xylosandrus* by Wood and Bright (1992) have subcontiguous or contiguous procoxae, along with many other characters that set them apart from the species originally included in the genus. Since Wood and Bright gave no discussion of characters supporting their new combinations, it is difficult to ascertain their reasoning. Since 1992, additional species have been described in or transferred to *Xylosandrus*, only some of which fit the characters that originally defined the genus (Beaver 1998; Saha et al. 1992; Wood 2007; Dole and Beaver 2008).

The incorrect placement of many species within *Xylosandrus* has created some taxonomic confusion between *Xylosandrus* and the genera *Amasa* Lea (1893) and *Cnestus* Sampson (1911). In addition to this, the recent resurrection of the genus *Anisandrus* Ferrari (1867) has highlighted similarities between it and several species of *Xylosandrus* (Hulcr et al. 2007). In their review of the Australian species of *Xylosandrus*, Dole and Beaver (2008) made tentative steps toward correcting the taxonomy of *Xylosandrus* by defining characters that separate *Xylosandrus* (*sensu stricto*) from *Cnestus* and transferring two species, *Cnestus pseudosolidus* (Schedl) and *C. solidus* (Eichhoff), from *Xylosandrus* to *Cnestus*.

Xylosandrus sensu stricto can be distinguished from other xyleborine genera by the following combination of characters: stout body, usually about twice as long as wide, widely separated procoxae, flat scutellum that is flush with the surface of elytra, and obliquely truncate antennal club with the first segment forming a circular costa and dense pubescence on the oblique portion of the club (Reitter 1913; Browne 1963; Bright 1968; Wood 1986; Hulcr et al. 2007; Dole and Beaver 2008).

Amasa can best be distinguished from *Xylosandrus* by its antennal club, which is oval, not truncate, with prominent 1st and 2nd segments, separated by sutures that are either visible on both the anterior and posterior face or entirely covered by pubescence (Lea 1893; Wood 1986; Hulcr et al. 2007). In all *Xylosandrus*, the antennal club is obliquely truncate, with the first segment forming a circular costa, lacking sutures posteriorly and with segment 1 covering the entire posterior face. *Amasa* also have contiguous procoxae (Lea 1893; Wood 1986; Hulcr et al. 2007). In all *Xylosandrus* (*sensu stricto*), the procoxae are separated by an intercoxal piece that is at least half the width of the coxae.

Anisandrus can be distinguished from *Xylosandrus* by the contiguous procoxae (Hulcr et al. 2007). The lateral margins of the protibae of *Anisandrus* are armed with six or seven socketed teeth. In *Xylosandrus* (*sensu stricto*) there are always only four or five socketed teeth on the lateral margin of the protibiae. *Anisandrus* species also have pronotal lateral margins that are rounded, a character which separates them from *Cnestus*, which has carinate lateral margins (Hulcr et al. 2007). *Xylosandrus* (*sensu stricto*) contains species with both rounded and carinate lateral margins of the pronotum.

Cnestus can be distinguished from *Xylosandrus* by the subcontiguous procoxae (Sampson 1911; Hulcr et al. 2007). *Cnestus* also have antennae with four funicular segments, whereas *Xylosandrus* species have five. Additionally, in *Cnestus* the anterior margin of the pronotum bears

4 or fewer asperities, with a pair of coarse asperities medially, and the pronotum is often produced anteriorly. In *Xylosandrus* the anterior margin of the pronotum bears six or more smaller asperities of approximately equal size and is never produced anteriorly. Many species of *Cnestus* have elytra that are wider than they are long, a character which is never observed in *Xylosandrus sensu stricto*.

Recent taxonomic work has examined the classification of xyleborine genera within a phylogenetic context (Jordal et al. 2000; Jordal 2002; Hulcr et al. 2007; Dole et al. 2010). A cladistic review of the generic taxonomic characters of Xyleborina recovered a monophyletic *Xylosandrus*, but it is important to note that this study did not include species with morphologies that deviate from the *sensu stricto* concept of the genus (Hulcr et al. 2007). Dole and Beaver (2008) were the first to treat the classification of problematic *Xylosandrus* species by defining characters that distinguish *Xylosandrus* from *Cnestus*. Phylogenetic analyses of DNA sequence data have also recovered a non-monophyletic *Xylosandrus*. Jordal (2002) used the nuclear gene Elongation Factor -1α (EF-1 α) to test the monophyly of the Xyleborina and, while the subtribe was recovered as monophyletic, *Xylosandrus* was found to be paraphyletic with respect to *Cnestus*. Phylogenetic reconstruction of a subset of *Xylosandrus* taxa using data from mitochondrial and nuclear genes recovered a polyphyletic *Xylosandrus* with the placement of *Anisandrus* and *Cnestus* among *Xylosandrus* species (Dole et al. 2010). In addition, several *Xylosandrus* species were placed within the "*Anisandrus*" and "*Cnestus*" clades with strong support (e.g., 100% bootstrap support), further indicating the need for a taxonomic revision of *Xylosandrus*.

BIOGEOGRAPHY

Xylosandrus is widely distributed in primarily tropical, but also in temperate regions worldwide. Whereas the inclusion of the problematic species discussed above does not change the overall distribution in terms of biogeographical regions, the biogeography discussed herein will pertain to *Xylosandrus* as it is defined in this taxonomic revision (Table 1). Three species of *Xylosandrus* have almost circumtropical distributions: *X. compactus*, *X. crassiusculus*, and *X. morigerus*. A fourth species, *Xylosandrus germanus* is less widely distributed, occurring in the Nearctic Region, Oceania, the Oriental Region, and the Palearctic Region. These four species were all introduced as exotic invasive species into temperate regions of the world. Apart from these species, *Xylosandrus* has a high level of regional endemism, with 71% of species occurring in only one biogeographical region. The Oriental Region is the most species rich, with 76% of *Xylosandrus* species present and a high occurrence of endemic species. The next richest is the Australian Region, with 29% of *Xylosandrus* species present. The Afrotropical Region and Oceania each contain 13%, and the Palearctic Region contains 16% of *Xylosandrus* species. Contrary to its tendency towards remarkable levels of scolytine species diversity, the Neotropical Region contains the same number of *Xylosandrus* species as the Nearctic (where the vast majority of species are introduced). This is congruent with the biogeography of the rest of Xyleborina, which tend to have their highest levels of diversity in the Old World Tropics (Beaver 1979; Wood and Bright 1992).

NATURAL HISTORY

As is typical of ambrosial feeding scolytines, *Xylosandrus* beetles are usually not host specific (Beaver 1979). Known host plants are listed for each species herein. All xyleborine beetles are haplodiploid, inbreeding and sexually dimorphic (Figs. 33 and 34). The haploid males are dwarfed, flightless and bear little resemblance to their female counterparts. All *Xylosandrus* species are xylomycetophagous. The female carries ambrosial fungi within a mycangium between the pronotum and mesonotum. Colonization of a host tree begins when a female beetle locates a suitable host and initiates gallery construction. As she bores into the tree, the female inoculates the woody tissue lining the gallery tunnels with a suite of microorganisms, including the ambrosial fungi. Once the fungi have begun to grow along the walls of the gallery, the female beetle lays eggs in small clusters at the end of the main tunnel. *Xylosandrus* larvae and adults feed exclusively on the ambrosial fungi. If the establishing female was unmated, she will produce only male offspring. In this case, as soon as they have pupated into adults, the flightless and dwarfed males (Fig. 34) may mate with their mother to produce female offspring. If the establishing female had mated prior to gallery construction, she will produce both male and female offspring, but with a highly skewed sex ratio (Kirkendall 1993). In Xyleborina beetles, the female to male sex ratio has been observed to be as high as 30:1 (Bright 1968; Kirkendall 1993). When both male and female offspring have been produced, the males will mate with their sisters to produce the next generation of beetles (Kirkendall 1993).

TABLE 1: Biogeographic distribution of *Xylosandrus* species: ● = present; ▲ = present as introduced species.

Species	Afrotropical Region	Australian Region	Nearctic Region	Neotropical Region	Oceania	Oriental Region	Palearctic Region
X. abruptulus		●					
X. adherescens						●	
X. amputatus n. comb.						●	
X. arquatus						●	
X. assequens						●	
X. beesoni						●	
X. borealis						●	●
X. boreensis n. sp.						●	
X. brevis						●	●
X. compactus	●		▲	▲	●	●	
X. corthyloides						●	
X. crassiusculus	●	●	▲	▲	●	●	▲
X. curtulus			●	●			
X. derupteterminatus						●	
X. deruptulus						●	
X. discolor		●			●	●	
X. diversepilosus						●	
X. eupatorii						●	
X. ferinus						●	
X. germanus			▲		●	●	▲
X. hirsutipennis	●						
X. huleri n. sp.		●					
X. jaintianus						●	●
X. mancus	●					●	
X. mediocris						●	
X. mesuae		●				●	
X. metagermanus						●	
X. mixtus n. comb.		●					
X. monteithi		●					
X. morigerus	●	●		▲	●	●	▲
X. nanus					●		
X. pusillus						●	
X. pygmeaus						●	
X. queenslandi		●					
X. rotundicollis n. comb.		●					
X. russulus n. comb.		●					
X. subsimiliformis						●	
X. subsimilis						●	
X. terminatus						●	
X. woodi		●					

MATERIALS AND METHODS

Approximately 1,300 specimens were studied from entomological collections. The following acronyms are used for collections referenced in the text:

AMNH American Museum of Natural History, New York, New York, USA.
BMNH The Natural History Museum, London, United Kingdom.
BPBM Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CAS California Academy of Sciences, San Francisco, California, USA.
CSCA California State Collection of Arthropods, Sacramento, California, USA.
FICB Forest Research Centre, Lae, Papua New Guinea.
FMNH Field Museum of Natural History, Chicago, Illinois, USA.
FRCS Forest Research Centre, Sabah, Sandakan, Malaysia.
FRI Indian Forest Research Institute, Dehra Dun, Uttar Pradesh, India.
IRSNB Institut Royal des Sciences Naturelles de Belgique, Belgium, Brussels.
IZM Institute of Zoology, Moscow, Russia.
MNB Museum fur Naturkunde der Humbolt University, Berlin, Germany.
MRCB Musee Royal de l'Afrique Centrale, Tervuren, Belgium.
MSUC Michigan State University Collection, East Lansing, Michigan, USA.
MTD Museum für Tierkunde, Dresden, Germany.
MZLU Lund University, Lund, Sweden.
MZUSP Museum de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil.
NHMW Naturhistorisches Museum Wien, Wien, Austria.
NHR Naturhistorisk Riksmuseet, Stockholm, Sweden.
NZSI Zoological Survey of India, National Zoological Collection, Calcutta, India.
RAB Roger A. Beaver, personal collection, Chiang Mai, Thailand.
UCDC R.M. Bohart Museum of Entomology, University of California, Davis, California, USA.
USNM National Museum of Natural History, Washington, D.C., USA (Including Stephen L. Wood Collection).
ZFMK Zoologische Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
ZMAN Universiteit van Amsterdam, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam, Netherlands.

Specimen label data are given verbatim. The biogeographical regions used in the species distributions are based on Wallace's maps with the following modifications: The Philippines are listed as part of the Oriental Region, instead of the Australian Region; the southern limit of the Palearctic Region in Africa is delimited by the Sahara Desert, instead of the Tropic of Cancer; and the entire Arabian Peninsula is listed as part of the Palearctic. Plant host species were compiled from the following publications: Bright and Skidmore (1997, 2002), Cibrián et al. (1995), Ohno (1990), Schedl (1963a), Wood and Bright (1992). Hosts recorded since the publication of Bright and Skidmore (2002) were collected from the literature by the authors and provided by Dr. Don Bright (pers. com.). Plant author names, when missing, were added using the International Plant Names Index (www.ipni.org).

Morphological Characters

A total of 43 external morphological characters (24 binary, 19 multistate) was coded and used in the phylogenetic analysis. Morphological characters were scored for females only, since the morphological classification of Xyleborina beetles is based entirely on females and males are rare or unknown for many species. Characters were scored for the 52 species of *Xylosandrus* sensu Wood and Bright (1992) (Appendix 1). In order to test the generic limits of *Xylosandrus*, a diversity of taxa were included in the morphological analysis: three *Anisandrus*, nine *Amasa*, three

Cnestus, one *Coccotrypes* and three *Xyleborus* species (Appendix 1). Characters coded were distributed as follows: two habitus characters (5 states), five head characters (14 states), 14 pronotal characters (35 states), two elytral characters (5 states), and 20 elytral declivity characters (51 states). Characters that were ambiguous or difficult to see on the specimen(s) examined were coded as "?" and treated as missing data. Inapplicable characters were coded as "?" and treated as missing data. All characters were treated as non-additive and unweighted in the phylogenetic analysis.

The following morphological characters and character states were used in the phylogenetic analysis. The character data matrix (Appendix 1) was prepared and coded using the program MX (Yoder et al. 2006-Present).

Habitus

1. *Body ratio*
    - 0 = less than 2.0 times longer than wide
    - 1 = more than 2.0 times longer than wide
2. *Pronotal to elytra color*
    - 0 = roughly the same color
    - 1 = elytra distinctly darker than pronotum
    - 2 = overall, same color, but elytra with testaceous patches

Head

3. *Frons sculpture*
    - 0 = punctate
    - 1 = finely granulate
    - 2 = reticulate or rugose
    - ? = ambiguous or difficult to see
4. *Frons median keel*
    - 0 = absent
    - 1 = present
    - ? = ambiguous or difficult to see
5. *Antennal funicular segment count*
    - 0 = 4-segmented
    - 1 = 5-segmented
    - 2 = 6-segmented
    - ? = ambiguous or difficult to see
6. *Antennal club type*
    - 0 = anntenal club without first segment forming a circular costa
    - 1 = anntenal club with first segment forming a circular costa that is closed anteriad
    - 2 = anntenal club with first segment forming a circular costa that is closed posteriad
    - ? = ambiguous or difficult to see
7. *Segments visible on posterior face of antennal club*
    - 0 = segments 2 and 3 not visible, segment 1 covering whole face
    - 1 = segment 2 visible, segment 1 covering most of face
    - 2 = segments 1, 2, and 3 visible on face
    - ? = ambiguous or difficult to see

Pronotum

8. *Pronotum ratio*
    - 0 = ratio of pronotal length to width ≤ 0.9
    - 1 = ratio of pronotal length to width = 1.0
    - 2 = ratio of pronotal length to width ≥ 1.1
9. *Pronotal type dorsal*
    - 0 = rounded (type 1, Huler et al. 2007)
    - 1 = basic (type 2, Huler et al. 2007)

10. *Pronotal type laterally*
    0 = basic (type 0, Hulcr et al. 2007)
    1 = rounded (type 1, Hulcr et al. 2007)
    2 = prolonged anteriorly (type 9, Hulcr et al. 2007)
    3 = prolonged posteriorly (type 8, Hulcr et al. 2007)
11. *Pronotal vestiture*
    0 = erect, hair-like setae
    1 = semi-appressed, hair-like setae
12. *Pronotal basal setae*
    0 = glabrous, without setae (except for mycangium, when present)
    1 = moderately setose, with basal setae being less dense than anterior
    2 = densely setose, with basal setae being at least as dense as anterior
13. *Pronotal mycangial setae*
    0 = absent
    1 = present
    ? = ambiguous
14. *Pronotal basal sculpture*
    0 = punctate
    1 = asperate-granulate
15. *Pronotal basal sculpture density*
    0 = moderate sculpture, punctures or granules separated by a distance greater than their size
    1 = dense sculpture, punctures or granules separted by a distance equal to or less than their size
16. *Pronotal anterior serrations count*
    0 = 4 or fewer serrations
    1 = 6 or more serrations
17. *Coarse median pair of serrations on anterior pronotum*
    0 = absent
    1 = present
    ? = only two anterior serrations present
18. *Pronotal anterior margin produced*
    0 = not produced
    1 = produced
19. *Pronotal lateral carina*
    0 = absent
    1 = present
20. *Procoxal separation*
    0 = widely separated, intercoxal piece at least ⅓ the width of coxae
    1 = narrowly separated to subcontiguous
    2 = contiguous
    ? = procoxae not visible
21. *Protibial teeth*
    0 = 4 or 5 socketed teeth
    1 = 6 socketed teeth
    2 = 7 socketed teeth
    3 = 8 socketed teeth
    ? = ambiguous or difficult to see

Elytra

22. *Elytral ratio*
    0 = ratio of elytral length to width ≥ 1.1
    1 = ratio of elytral length to width = 1.0
    2 = ratio of elytral length to width ≤ 0.9

23. *Discal interstrial sculpture distribution*
    0 = uniseriate
    1 = multiseriate, including biseriate

Elytral Declivity

24. *Declivital origin*
    0 = declivity originating less than ⅓ the length of elytra from base
    1 = declivity originating ≥ ½ the length of elytra from base
25. *Decilivital slope*
    0 = elytral disc gradually curving into declivity
    1 = declivital face abrupt and steeply separated from disc
26. *Declivital shape*
    0 = not circular: oval or oblong
    1 = circular
27. *Declivital surface*
    0 = convex
    1= flattened
    2 = concave, at least in part
28. *Posterolateral declivital margin*
    0 = absent, rounded
    1 = granulate
    2 = carinate
    3 = serrate
29. *Declivital carina length*
    0 = carina not extending beyond 7th interstriae
    1 = carina extending beyond 7th interstriae, forming a circumdeclivital ring
    ? = absent
30. *Declivital striae count*
    0 = 2 striae visible on declivity
    1 = 3 striae visible on declivity
    2 = 4 striae visible on declivity
    3 = 5 striae visible on declivity
    4 = 6 striae visible on declivity
    ? = ambiguous
31. *Declivital strial impression*
    0 = not impressed
    1 = impressed
32. *Declivital strial sculpture*
    0 = punctate
    1 = granulate
33. *Declivital strial sculpture distribution*
    0 = seriate
    1 = confused
34. *Declivital strial setae type*
    0 = absent
    1 = hair-like
    2 = scale-like
    ? = ambiguous
35. *Declivital strial setae length*
    0 = length less than or equal to the width of second declivital interstriae
    1 = length greater than the width of second declivital interstriae
    2 = length at least 2 times the width of second declivital interstriae

? = absent or ambiguous

36. *Declivital strial setae profile*
    0 = appressed or semi-appressed
    1 = erect
    ? = absent or ambiguous
37. *Declivital interstrial sculpture*
    0 = punctate
    1 = coarsely granulate
    2 = finely granulate
38. *Declivital interstrial sculpture distribution*
    0 = uniseriate
    1 = multiseriate, including biseriate
39. *Declivital interstrial setae type*
    0 = absent
    1 = hair-like
    2 = scale-like
    ? = ambiguous
40. *Declivital interstrial setae length*
    0 = length less than or equal to the width of second declivital interstriae
    1 = length greater than the width of second declivital interstriae
    2 = Length at least twice the width of second declivital interstriae
    ? = absent or ambiguous
41. *Declivital interstrial setae profile*
    0 = appressed or semi-appressed
    1 = erect
    ? = absent, ambiguous
42. *First interstriae elevated at apex of elytra*
    0 = not elevated
    1 = elevated
43. *Granules or tubercles near apex of first interstriae*
    0 = absent
    1 = present

Molecular Characters

The molecular data set used herein (Dole et al. 2010) is comprised of multiple gene loci, chosen for their complementary phylogenetic signals at varying nodal depths: 28S rDNA; the mitochondrial gene cytochrome oxidase I (COI); and the nuclear protein-coding genes argenine kinase (ArgK), CAD (rudimentary), and Elongation Factor -1α (EF-1α). For extraction, sequencing and alignment protocols see Dole et al. (in review). For our combined analysis, we used the molecular data set aligned manually with reference to a scolytine-specific secondary structure model (Jordal et al. 2008). The resulting combined data set included only taxa for which both morphological and molecular data were available (Table 3). This combined data set includes 27 taxa, representing 15 *Xylosandrus* species, 12 species belonging to the genera *Amasa*, *Anisandrus*, *Cnestus*, *Xyleborus*, and the oustgroup genus *Coccotrypes* (Table 3).

PHYLOGENETIC ANALYSIS

Phylogenetic analysis of the morphological data set was conducted with the software TNT (Goloboff et al. 2003). A new technology driven search was employed for the parsimony analysis with all search modules employed: sectorial search (RSS and CSS), ratchet, drift, and tree fusing.

Default TNT setting were used, with the following exceptions: tree fusion was conducted globally after every hit and the search was set to end after the minimal tree length was found 10 times. Traditional (heuristic) search methods were then used to conduct tree bisection and reconnection branch swapping on the 51 most parsimonious trees found in the new technology search. Maximum trees being held by TNT was set to 10,000. Bootstrap support values were calculated by performing 1,000 pseudo-replicates with simple sequence addition in the program Winclada (Nixon 1999).

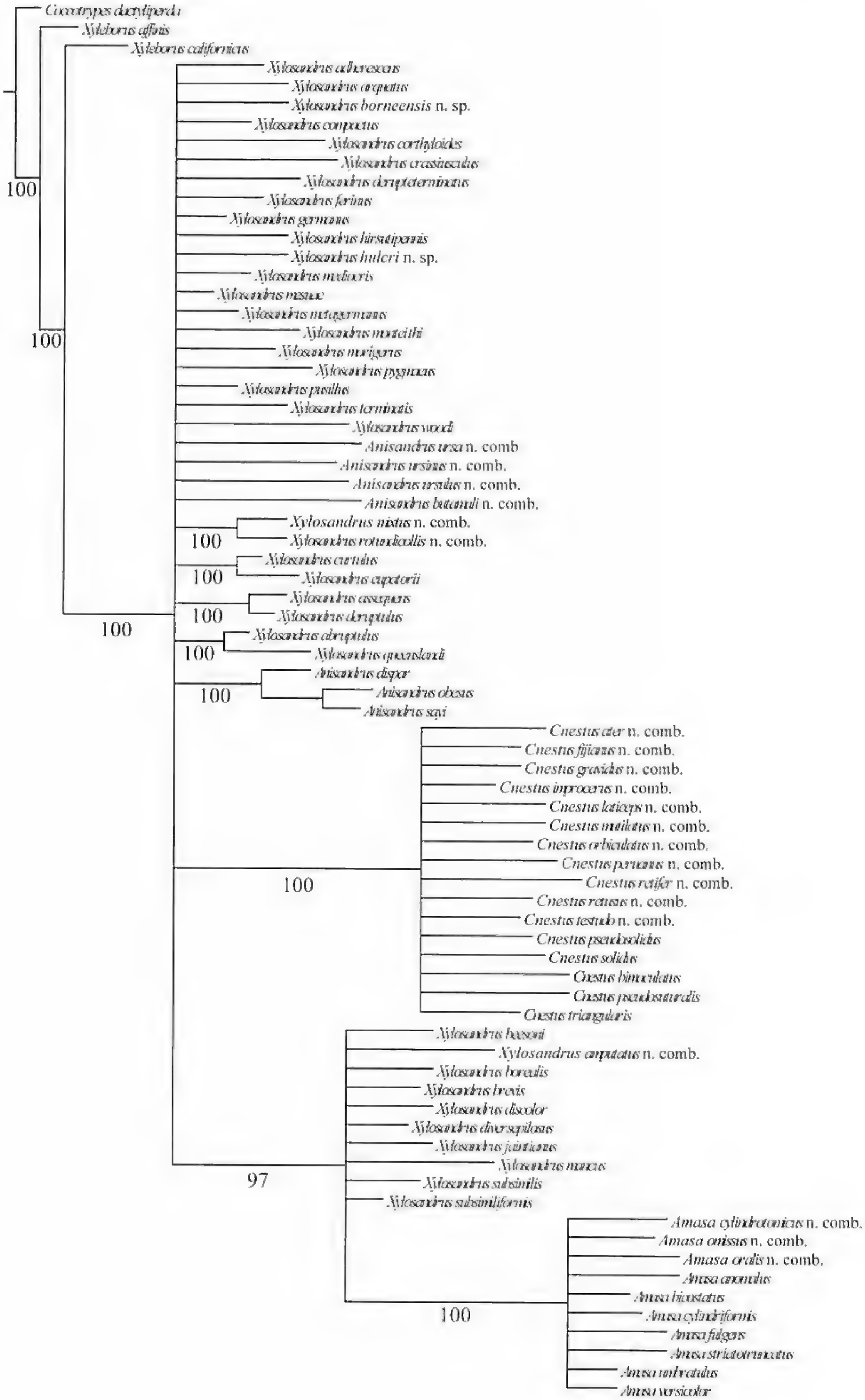
Phylogenetic analysis of the combined data set was conducted with the software PAUP* (Swofford 2002). A heuristic search was employed with 300 random stepwise addition replicates using PAUP* default settings. Gaps were treated as missing data in the analysis. Bootstrap values were calculated by performing 1,000 pseudo-replicates with simple addition sequence in PAUP*. Bremer support values for each data partition were calculated by constructing a constraint tree with the software TreeRot (Sorensen 1996) followed by subsequent analysis with PAUP*.

Results

Xylosandrus was recovered as polyphyletic by analyses of both the morphological and the combined data set. Phylogenetic analysis of the morphological data set produced 10,000+ equally parsimonious trees of 306 steps (max trees in TNT set to 10,000) (Fig 1). The strict consensus tree was mostly unresolved, but recovered several clades with high support values. The monophyly of the clade containing *Amasa*, *Anisandrus*, *Cnestus*, and *Xylosandrus* with respect to the genus *Xyleborus* was recovered with 100% bootstrap support. The unresolved placement of the "*Amasa*", *Anisandrus*, and "*Cnestus*" clades, as well as the placement of several species of *Xylosandrus* within these clades, was responsible for rendering *Xylosandrus* paraphyletic. While morphology did not resolve their phylogenetic placement, the data did support the monophyly of the "*Amasa*" and "*Cnestus*" clades and the inclusion of several *Xylosandrus* species within them. These clades were both recovered with 100% bootstrap support. *Anisandrus* was recovered as monophyletic with 100% bootstrap support. The Consistency Index (CI) indicates that the occurrence of homoplasy is high in the morphological data set (CI = 0.190). Furthermore, the Retention Index (RI) indicates that character state changes are occurring predominantly on the internal nodes (RI = 0.671).

Phylogenetic analysis of the combined data set recovered a single most parsimonious tree of 4524 steps (Fig. 2). This tree was well resolved, with high support values (e.g. $\geq$ 90% boostrap support) toward the terminal nodes and poorer support (e.g. $\leq$ 74 % bootstrap support) for the deeper relationships among the clades. The placement of the "*Anisandrus*", and "*Cnestus*" clades, the inclusion of several *Xylosandrus* species within these clades, as well as the placement of *Xylosandrus mancus* and *X. discolor* in a clade with *Amasa* and *Xyleborus*, rendered *Xylosandrus* polyphyletic. The low support for deeper nodes made it impossible to determine the phylogenetic relationships among *Xylosandrus*, *Amasa*, *Anisandrus*, *Cnestus*, and *Xyleborus*. However, the placement of several species of *Xylosandrus* within the "*Anisandrus*" and "*Cnestus*" clades had very strong support (e.g., 100% bootstrap support). The genus *Amasa* and a *Xylosandrus sensu stricto* clade (containing the type species *X. morigerus*) were also recovered with 100% bootstrap support.

Homoplasy as measured by CI and RI indicated that homoplasy was lowest for the 28S data partition (Table 2). The nuclear protein-coding genes ArgK, CAD, and EF-1α had similar CI's (0.474–0.522) and RI's (0.460–0.600). The mitochondrial gene COI had the highest level of homoplasy (CI = 0.265, RI = 0.246). The low RI value for COI indicates that the character state changes for this gene largely occurred towards the terminal nodes of the tree. The morphological data demonstrated lower levels of homoplasy in the combined analysis (CI = 0.346) than it did when analyzed alone (CI = 0.200). However, the RI observed for the morphological data was lower in


Coccotrypes dactyliperda
Xyleborus affinis
Xyleborus californicus
Xylosandrus adherescens
Xylosandrus arquatus
Xylosandrus borneensis n. sp.
Xylosandrus compactus
Xylosandrus corthyloides
Xylosandrus crassiusculus
Xylosandrus derupteterminatus
Xylosandrus ferinus
Xylosandrus germanus
Xylosandrus hirsutipennis
Xylosandrus hulcri n. sp.
Xylosandrus mediocris
Xylosandrus mesuae
Xylosandrus metagermanus
Xylosandrus monteithi
Xylosandrus morigerus
Xylosandrus pygmaeus
Xylosandrus pusillus
Xylosandrus terminatus
Xylosandrus woodi
Anisandrus ursa n. comb
Anisandrus ursinus n. comb.
Anisandrus ursulus n. comb.
Anisandrus butamali n. comb.
Xylosandrus mixtus n. comb.
Xylosandrus rotundicollis n. comb.
Xylosandrus curtulus
Xylosandrus eupatorii
Xylosandrus assequens
Xylosandrus deruptulus
Xylosandrus abruptulus
Xylosandrus queenslandi
Anisandrus dispar
Anisandrus obesus
Anisandrus sayi
Cnestus ater n. comb.
Cnestus fijianus n. comb.
Cnestus gravidus n. comb.
Cnestus improcerus n. comb.
Cnestus laticeps n. comb.
Cnestus mutilatus n. comb.
Cnestus orbiculatus n. comb.
Cnestus parianus n. comb.
Cnestus retifer n. comb.
Cnestus retusus n. comb.
Cnestus testudo n. comb.
Cnestus pseudosolidus
Cnestus solidus
Cnestus bimaculatus
Cnestus pseudosuturalis
Cnestus triangularis
Xylosandrus beesoni
Xylosandrus amputatus n. comb.
Xylosandrus borealis
Xylosandrus brevis
Xylosandrus discolor
Xylosandrus diversepilosus
Xylosandrus jaintianus
Xylosandrus mancus
Xylosandrus subsimilis
Xylosandrus subsimiliformis
Amasa cylindrotomicus n. comb.
Amasa omissus n. comb.
Amasa oralis n. comb.
Amasa anomalus
Amasa bicostatus
Amasa cylindriformis
Amasa fulgens
Amasa striatotruncatus
Amasa truncatulus
Amasa versicolor
100
100
100
100
100
100
100
100
100
97
100

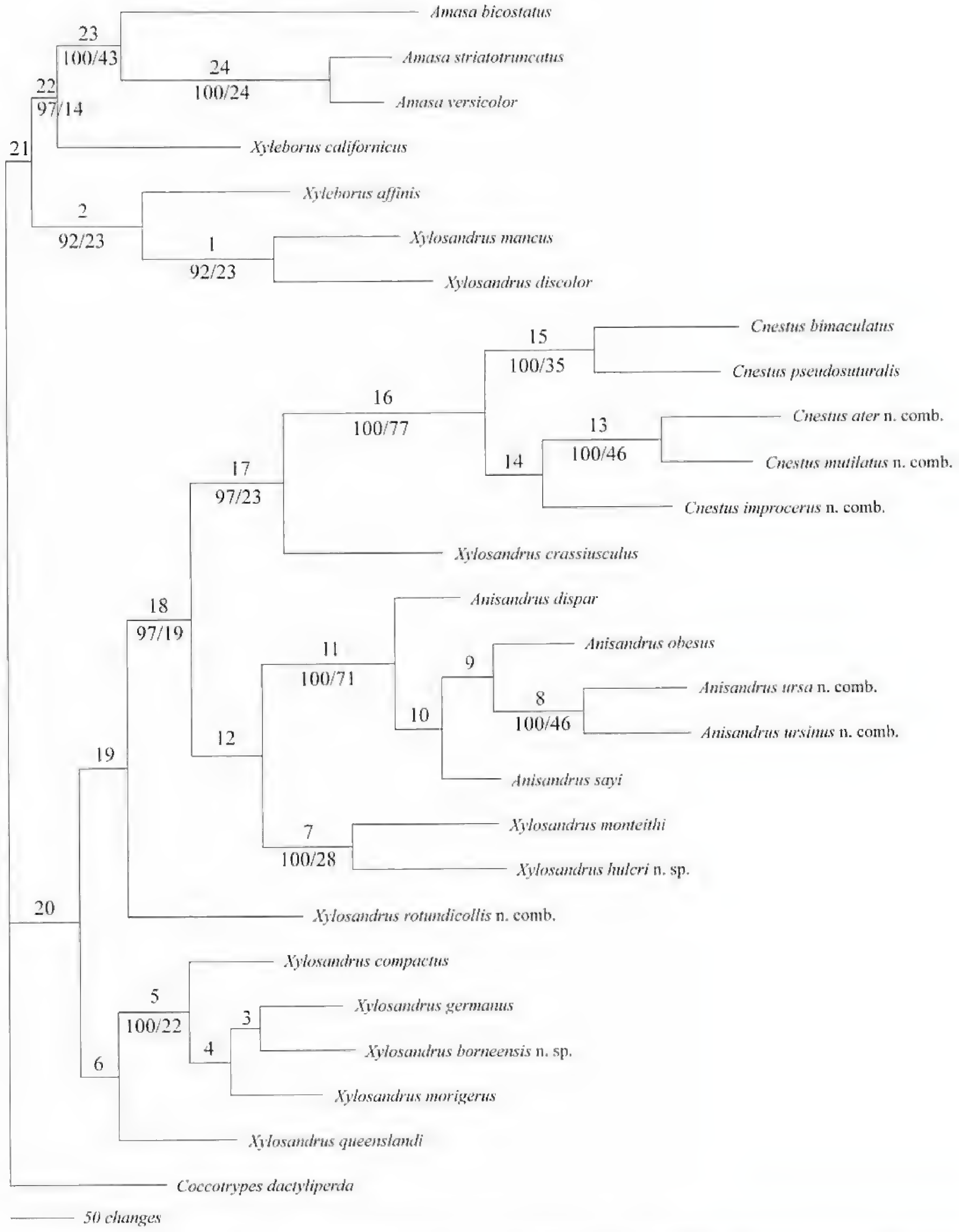


FIGURE 1 (left). Strict consensus of 10,000 most parsimonious trees found in parsimony analysis of the morphological data martrix. Bootstrap values are given below the nodes for clades with support ≥ 90%.

FIGURE 2 (above). Most parsimonious tree found in the analysis of the combined data matrix. Node numbers given above branches and bootstrap support/Bremer support values given below.

the combined analysis (RI = 0.492), indicating that the occurrence of character state changes shifted more toward the terminal nodes when the data were combined with molecular data. Overall, 28S gave the highest Bremer support values, with CAD having the next highest values (Table 3). Interestingly, the overall Bremer support values for COI and morphology were similar.

TABLE 2: Contribution of data partitions to the data matrix and to the resolution of the most parsimonious tree found in the analysis of the combined data set.

	Matrix Size	Variable Sites	Informative Sites	Gaps	Contribution to Tree Length	Consistency Index (CI)	Retention Index (RI)	Mean Branch Length
EF-1α	555	151	102	N/A	371	0.493	0.46	7.98
COI	585	247	219	N/A	1549	0.265	0.246	31.39
ArgK	594	195	153	N/A	529	0.522	0.6	11.04
CAD	714	226	172	N/A	607	0.474	0.527	12.72
28S	1048	463	335	473	1283	0.631	0.759	26.29
Morphology	43	43	40	N/A	185	0.346	0.492	3.94
Combined	3539	1325	1021	473	4524	0.449	0.536	93.37

DISCUSSION

All analyses conducted herein recovered a polyphyletic *Xylosandrus*, with the present classification of the genus containing species from at least five different genera: *Xylosandrus*, *Amasa*, *Anisandrus*, *Cnestus*, and *Euwallacea*. These findings are consistent with those of other studies of *Xylosandrus* (Jordal 2002; Dole and Beaver 2008; Dole et al. 2010). Separate and combined analyses of morphological and molecular data sets have recovered the following clades with high support values: "*Anisandrus*", "*Amasa*", "*Cnestus*" and "*Xylosandrus sensu sticto*" (Dole et al. 2010). However, even a data set combining morphology and five gene partitions was not sufficient to resolve the relationships among these genera (Fig. 2). Despite this, these trees provide a valuable framework with which to revise the present classification of *Xylosandrus*.

Amasa Clade

The "*Amasa*" clade has been consistently recovered by all parsimony analyses (Bayesian and POY analyses of molecular data recovered an unresolved or polyphyletic *Amasa*, with respect to *Xyleborus*) (Dole et al. 2010) (Figs. 1 and 2). The genus is rendered monophyletic by the inclusion of three *Xylosandrus* species: *X. cylindrotomicus*, *X. omissus*, and *X. oralis* (Fig. 1). The placement of these species within *Amasa* is supported by morphological characters (Fig. 3). Similarly, the species *A. mixtus* and *A. amputatus* were included among *Xylosandrus* species, rather than *Amasa*, by the analysis of the morphological data set. The transfer of these species into *Xylosandrus* is consistent with the characters defining *Xylosandrus sensu stricto*. The combined phylogenetic analyses have indicated that *Amasa* is more closely related to *Xyleborus* than it is to *Anisandrus*, *Cnestus*, and *Xylosandrus*. Thus, it appears that confusion between *Xylosandrus* and *Amasa* was simply the result of taxonomic error and not an indication of close phylogenetic relationship.

TABLE 3: Partition branch support for the most parsimonious tree found by the analysis of the combined data set. Node numbers refer to Figure 2.

				Gene Partition			
	Ef-1α	**COI**	**ArgK**	**CAD**	**28S**	**Morphology**	**Combined**
node							
1	3.00	2.00	5.00	8.00	0.00	5.00	23
2	3.00	2.00	5.00	8.00	0.00	5.00	23
3	1.00	4.00	2.00	0.00	1.00	-1.00	7
4	0.00	-2.00	2.00	4.00	-2.00	0.00	2
5	8.00	-1.50	7.50	11.00	-1.00	-2.00	22.00
6	3.00	0.00	-1.00	0.00	4.00	0.00	6.00
7	2.00	0.00	-4.00	-2.00	36.00	-4.00	28.00
8	0.00	5.00	0.00	11.00	25.00	5.00	46.00
9	0.00	2.00	-3.00	-4.00	15.00	-4.00	6.00
10	0.00	2.00	-3.00	-4.00	15.00	-4.00	6.00
11	5.00	6.00	2.00	-1.00	63.00	-4.00	71.00
12	2.00	-1.00	-1.00	-1.00	2.00	0.00	1.00
13	5.00	0.00	15.00	10.00	11.00	5.00	46.00
14	3.00	-2.00	1.00	-2.00	2.00	1.00	3.00
15	0.00	1.00	10.00	15.00	8.00	1.00	35.00
16	13.00	5.67	29.67	13.33	8.33	7.00	77.00
17	3.00	2.00	5.00	8.00	0.00	5.00	23.00
18	-1.00	-3.00	-3.00	0.00	26.00	0.00	19.00
19	2.00	0.00	1.00	0.00	5.00	1.00	9.00
20	0.00	-0.50	4.00	5.00	2.00	2.50	13.00
21	2.00	-2.00	-1.00	2.00	5.00	0.00	6.00
22	3.00	-2.00	0.00	10.00	3.00	0.00	14.00
23	8.50	2.50	-0.50	18.50	3.00	11.00	43.00
24	0.00	11.00	7.00	7.00	2.00	-3.00	24.00
Total	**65.50**	**31.17**	**79.67**	**116.83**	**233.33**	**26.50**	**442.00**

Anisandrus Clade

The "*Anisandrus*" clade has been recovered by all analyses that included molecular data (Dole et al. 2010) (Fig. 2). The only analysis that did not recover this clade was that of morphological data alone (Fig. 1). However, the membership of species included in this clade is consistent with characters that support the separation of *Anisandrus* from other Xyleborina genera (Hulcr et al. 2007) (Fig. 4). All other analyses recovered the "*Anisandrus*" clade with high support (100% boostrap support, Bayesian posterior probability of 100, and Bremer supports ranging from 22-67) (Dole et al. 2010) (Fig. 2; Table 3). The genus *Anisandrus* is rendered monophyletic by the inclusion of three *Xylosandrus* species: *X. ursa*, *X. ursinus*, *X. ursulus*. Transfer of these species to *Anisandrus* is also supported by the morphological characters that distinguish the genus (Hulcr et al. 2007). *Xylosandrus butamali* is a fourth species with the morphological characteristics of *Anisandrus* rather than those of *Xylosandrus*. This species was not available for DNA sequencing and was only included in the morphological analysis. This analysis placed *X. butamali* in a larger clade with the "*Anisandrus*" and "*Cnestus*" clades with 93% bootstrap support, but the relationships within this clade were unresolved in the strict consensus tree. Based on this phylogenetic evidence, in combination with the morphological characters that distinguish *Anisandrus*, we transfer *X. butamali* to *Anisandrus*.

Cnestus Clade

The "*Cnestus*" clade has been recovered by all phylogenetic analyses (Dole et al. 2010) (Figs. 1 and 2). The genus is rendered monophyletic by the inclusion of 11 *Xylosandrus* species: *X. ater*, *X. fijianus*, *X. gravidus*, *X. improcerus*, *X. laticeps*, *X. mutilatus*, *X. orbiculatus*, *X. peruanus*, *X. retifer*, *X. retusus*, and *X. testudo*. These are in addition to two species already transferred from *Xylosandrus* to *Cnestus* by Dole and Beaver (2008): *X. pseudosolidus* and *X. solidus*. The inclusion of these species in *Cnestus* is also supported by morphological characters used to distinguish the genus (Hulcr et al. 2007; Dole and Beaver 2008) (Fig. 5). Support values for the "*Cnestus*" clade were very high (100% bootstrap support, Bayesian posterior probability of 100, and Bremer supports ranging from 53-120).

The transfer of the above species from *Xylosandrus* to *Cnestus* is of some importance to scolytine control, considering the establishment of *X. mutilatus* as an invasive species in North America. The inclusion of *X. mutilatus* in *Cnestus* constitutes a new generic record for North America (Rabaglia et al. 2006). Likewise, the transfer of several South American species (*X. laticeps*, *X. peruanus*, *X. retifer*, *X. retusus*) to *Cnestus* establishes, for the first time, the presence of the genus in the Neotropics (Wood 2007).

Xylosandrus (*sensu stricto*) Clade

The "*Xylosandrus sensu stricto*" clade was consistently recovered by all analyses that included molecular data (Dole et al. 2010) (Fig. 2). The analysis of morphological data did not recover this clade, but the resolution for all *Xylosandrus* species not placed in clades with other genera was poor (Fig. 1). The "*Xylosandrus sensu stricto*" clade is comprised of (((*X. germanus* + *X. borneensis* n. sp.) *X. morigerus*) *X. compactus*). Given that it contains *X. morigerus*, the type species of *Xylosandrus*, this clade is the highest supported grouping of species belonging to *Xylosandrus* (*sensu stricto*) found by phylogenetic analyses of the genus. Support values for this clade were very high (100% bootstrap support, Bayesian posterior probabilities of 100, Bremer supports ranging from 21-28). The species included in this clade are morphologically consistent with the strict definition of the genus. This clade also contains three economically important species of *Xylosandrus*: *X. compactus*, *X. germanus*, and *X. morigerus*.

Xylosandrus (*sensu lato*)

The phylogenetic placement of the remaining *Xylosandrus* species was largely unresolved by these analyses. However, two clades were recovered by the combined data analysis with high support (≥ 92 % bootstrap support): *X. hulcri* n. sp. + *X. moteithi* and *X. discolor* + *X. mancus* (Fig. 2). The placement of a few species calls into question the monophyly of *Xylosandrus*, even after this revision. The placement of *X. crassiusculus* as sister to *Cnestus*, which has been recovered by multiple analyses with high support (≥ 97 % bootstrap support, Bayesian posterior probabilities of 100), would render the genus paraphyletic (Dole et al. 2010) (Fig. 2). Because of the wide distribution and economic importance of the species any taxonomic changes to *X. crassiusculus* should be made with strong phylogenetic support. A study of the species' relationship to other Xyleborina genera not considered in this analysis should be made before it is hastily established as a monotypic genus. Furthermore, *Xylosandrus crassiusculus* forms a morphologically distinct group with *X. hirsutipennis* and any analysis of its phylogenetic placement should consider this species as well. A phylogenetic study of Xyleborina genera is presently being completed and may shed more light on this taxonomic issue (Cognato et al., in prep.).

Several *Xylosandrus* species groups may require further consideration as the phylogenetics of Xyleborina genera is resolved. The species *X. amputatus, X. beesoni*, *X. borealis*, *X. brevis*, *X. discolor*, *X. diversepilosus*, *X. jaintianus*, *X. mancus*, *X. squamulatus*, *X. subsimilis*, and *X. subsimiliformis* all form a distinct morphological group with declivital faces that are steep and abruptly separated from the elytral disc. This grouping was recovered in a clade with *Amasa* by the analysis of morphological data with 97% bootstrap support. Phylogenetic analysis of the combined data set recovered a subset of these species (*X. discolor* + *X. mancus*) as more closely related to *Xyleborus affinis* (92% bootstrap support) and to a clade containing *Amasa* + *Xyleborus californicus* (64 % bootstrap support) than to *Xylosandrus*. Within this species group, *X. amputatus*, *X. mancus*, and *X. squamulatus* form perhaps the most distinct group of *Xylosandrus* species. These three species have lateral declivital margins with a carina or a raised rim of granules that extends beyond the 7th declivital interstriae, forming a circumdeclivital ring, a character often observed in *Amasa*. However, these species have *Xylosandrus*-type antennae and pronotal-mesonotal mycangia, two characters that are never observed in *Amasa*. Future work on the phylogenetics of *Xylosandrus* and the generic classification of Xyleborina should address these issues with more thorough taxon sampling and the expansion of DNA data sets.

Key to the Females of the Species of *Xylosandrus*

1 Margin of elytral declivity carinate or with a raised rim of granules 2
Margin of elytral declivity rounded, tuberculate, or serrate but without a continuous carina or rim 32
2 Margin of elytral declivity carinate to 7th interstriae 3
Margin of elytral declivity with carina extending beyond 7 th interstriae, forming a circum declivital ring 38
3 (2) Declivital face of elytra steep and abruptly separated from disc. 4
Elytral disc gradually curving into declivity 16
4 (3) Declivital striae punctate. Five or six striae visible on declivity. 5
Declivital striae granulate. Four or five striae visible on declivity 9
5 (4) Declivital striae impressed 6
Declivital striae not impressed. 7
6 (5) Elytral declivity with deeply impressed striae, giving the appearance of six distinct ridges on face. Six striae visible on declivity. Declivital striae with very appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae very finely granulate, giving the declivity a matte appearance, with erect, hair-like setae, shorter than the width of second declivital interstriae. Pronotum with a lateral costa, but not carinate. 1.5–1.6 mm long. Oriental Region . . . . *X. borneensis* **sp. nov.** (Fig. 12)
Elytral declivity with striae less impressed. Five striae visible on declivity. Declivital striae with erect or semi-erect, hair-like setae, longer than the width of second declivital interstriae. Interstiae more coarsely granulate, declivity shining. Pronotum with a lateral costa and carina. 1.3–1.5 mm long. Oriental Region. . . . . ***X. pygmaeus* (Eggers)** (Fig. 38)
7 (5) Elytral declivity flattened. Five striae visible on declivity 8
Elytral declivity convex. Six striae visible on declivity. Declivital striae with setae. Interstriae

uniseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 1.2–1.8 mm long. Afrotropical Region, Australian Region, Neotropical Region, Oceania, Oriental Region, Palearctic Region . . . . *X. morigerus* **(Blandford)** (Fig. 35)

8 (7) Interstriae uniseriate granulate, with erect, hair-like setae, less than the width of second declivital interstriae. Larger species, 2.0–2.3 mm long. Oriental Region. . . . . *X. derupteterminatus* **(Schedl)** (Fig. 18)

Interstriae uniseriate punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Smaller species, 1.5–1.9 mm long. Oriental Region. . . . . *X. terminatus* **(Eggers)** (Fig. 43)

9 (4) Declivity covered with a dense vestiture of appressed, flattened, scale-like setae. Striae and interstriae granulate. Pronotum granulate and pubescent basally. Lateral pronotum costate and carinate. Frons rugose. 2.6 mm long. Oriental Region. . . . . *X. subsimilis* **(Eggers)** (Fig. 42)

Declivital setae hair-like, not flattened 10

10 (9) Lateral pronotum costate and carinate 11

Lateral pronotum costate, but without a carina 14

11 (10) Pronotum uniformly convex dorsally. Declivital face convex. Smaller species, 1.5–2.0 mm long. Australian Region, Oceania, Oriental Region . . . . *X. discolor* **(Blandford)** (Fig. 20)

Pronotum with conspicuous summit on basal third. Declivital face flattened, convex, or depressed in areas. Larger species, 2.8–3.0 mm long 12

12 (11) Four striae visible on elytral declivity. Declivital interstriae without a row of longer, erect setae, bearing only a vestiture of short, appressed setae 13

Five striae visible on elytral declivity, with striae 4 and 5 forming a loop. Declivital interstriae with a single row of long, erect, hair-like setae, along with a dense vestiture of shorter appressed setae. 2.8–2.9 mm long. Oriental Region. . . . . *X. beesoni* **Saha, Maiti, and Chakraborti** (Illustrated in Saha et al. 1992)

13 (12) First and second declivital interstriae elevated toward apex, with depressed areas on each side of raised interstriae. Frons rugose, with a distinct median keel. 3.0 mm long. Oriental Region, Palearctic Region . . . . *X. jaintianus* **(Schedl)** (Fig. 27)

Declivital face flattened, without interstriae elevated toward apex. Frons punctate, without a distinct median keel. 2.8 mm long. Oriental Region . . . . *X. subsimiliformis* **(Eggers)** (Fig. 41)

14 (10) Declivital striae and interstriae granulate with appressed, hair-like setae. Interstriae in some species with a row of long, erect, hair-like setae in addition to appressed background vestiture. 15

Declivital striae coarsely granulate, without setae. Interstriae granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 1.8–2.3 mm long. Oriental Region. . . . . *X. diversepilosus* **(Eggers)** (Fig. 21)

15(14) Granules on interstriae dense and closely placed, giving the declivity a matte appearance. Smaller species, 2.0–2.1 mm long. Oriental Region. Palearctic Region. . . . . *X. borealis* **Nobuchi** (Fig. 11)

Granules on interstriae less densely and closely placed, giving the declivity a shining apprearance. Larger species, 2.5–2.8 mm long. Oriental Region, Palearctic Region . . . . *X. brevis* **(Eichhoff)** (Fig. 13)

16 (3) Declivital striae and interstriae densely, finely, and confusedly granulate. Pronotum of equal length and width. 17

Declivital striae and interstriae not densely, finely, and confusedly granulate. Striae punctate. Pronotum wider than long 18

17 (16) Pronotum with a lateral costa, but without a carina. Elytral disc multiseriate punctate. Six

striae visible on elytral declivity. Striae with erect, hair-like setae, shorter than the width of second declivital interstriae. Interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Frons rugose. 1.7–2.9 mm long. Afrotropical Region, Australian Region, Nearctic Region, Neotropical Region, Palearctic Region, Oceania, Oriental Region. . . . . ***X. crassiusculus*** **(Motschulsky)** (Fig. 16)

Pronotum with a lateral costa and carina. Elytral disc uniseriate punctate. Five striae visible on elytral declivity. Striae and interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Frons punctate. 1.9–2.2 mm long. Afrotropical Region . . . . ***X. hirsutipennis*** **(Schedl)** (Fig. 25)

18 (16) Pronotum with a lateral costa and carina. 19

Pronotum with a lateral costa, but without a carina 27

19 (18) At least first interstria on elytral disc multiseriate punctate 20

All interstriae on elytral disc uniseriate punctate. 21

20 (19) Elytral disc with interstriae densely punctured. Declivital interstriae multiseriate granulate. Declivital surface matte in appearance. Stouter species, 2.0 times longer than wide; elytra of equal length and width. 1.6–2.3 mm long. Oriental Region . . . . . ***X. assequens*** **Schedl** (Fig. 10)

Elytral disc with interstriae more sparely punctured, multiseriate only on first interstria. Declivital interstriae uniseriate granulate. Declivital surface shining. More elongate species, 2.2 times longer than wide; elytra 1.4 times longer than wide. 1.8 mm long. Oriental Region. . . . . ***X. deruptulus*** **(Schedl)** (Fig. 19)

21 (19) Declivital striae with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae 22

Declivital striae without setae 24

22 (21) Pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium. Elytra strongly arched from base to middle of declivity. 1.3–1.5 mm long. Nearctic Region, Neotropical Region . . . . ***X. curtulus*** **(Eichhoff)** (Fig. 17)

Pronotal disc more evenly pubescent, with a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium. Elytra more evenly arched from middle of disc to apex 23

23 (22) Body very stout, 1.9 times as long as wide. 1.5–1.7 mm long. Oriental Region . . . . ***X. pusillus*** **(Schedl)** (Fig. 36)

Body less stout, 2.3 times longer than wide. 1.4–1.9 mm long. Afrotropical Region, Nearctic Region, Neotropical Region, Oceania, Oriental Region. . . . . ***X. compactus*** **(Eichhoff)** (Fig. 14)

24 (21) Smaller species, 1.4 mm long. Pronotum of equal length and width. Declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae. Oriental Region . . . . ***X. mediocris*** **(Schedl)** (Fig. 29)

Larger species, 1.8–2.5 mm long 25

25 (24) Pronotum wider than long or of equal length and width. Pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium 26

Pronotum 1.1 times longer than wide. Pronotal disc more evenly pubescent, with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. 1.9–2.5 mm long. Nearctic Region, Oceania, Oriental Region, Palearctic Region. . . . . ***X. germanus*** **(Blandford)** (Fig. 24)

26 (25) Pronotum wider than long. Declivital interstriae uniseriate granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstria. 2.0 mm long. Oriental

Region. . . . . *X. adherescens* **Schedl** (Fig. 7)
Pronotum of equal length and width. Declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of second declivital interstria. 1.8–2.1 mm long. Oriental Region. . . . . *X. eupatorii* **(Eggers)** (Fig. 22)

27 (18) Body bicolored, with pronotum distinctly lighter than elytra or with a testaceous patch on elytra basally and laterally 28
Body uniformly colored, light to dark brown 31

28 (27) Pronotum and elytral apices dark brown, elytra with a testaceous patch basally and laterally. Elytral disc with interstriae multiseriate. Declivital interstriae multiseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae. 2.4–2.7 mm long. Australian Region . . . . *X. hulcri* **sp. nov.** (Fig. 26)
Pronotum distinctly lighter than elytra; elytra without a testaceous patch 29

29 (28)Smaller species, 1.1–1.3 mm long. Declivital striae with setae. Interstriae with erect, hair-like setae, longer than the width of second declivital interstriae. Australian Region, Oriental Region . . . . *X. mesuae* **(Eggers)** (Fig. 30)
Larger species, 1.6–2.5 mm long. Other characters varied 30

30 (29)Six striae visible on elytral declivity. Declivital striae with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae punctate. Body 2.3 times longer than wide. Larger species, 2.3–2.5 mm long. Oriental Region . . . . *X. arquatus* **(Sampson)** (Fig. 9)
Five striae visible on elytral declivity. Declivital striae without setae. Interstriae granulate. Smaller species, 1.6–1.8 mm long. Oriental Region . . . . *X. ferinus* **(Schedl)** (Fig. 23)

31 (27) Five striae visible on elytral declivity. Declivital striae with semi-appressed, hair-like setae. Interstriae multiseriate. Larger species, 2.6–2.7 mm long. Australian Region . . . . *X. mixtus* **(Schedl)** (Fig. 32)
Six striae visible on elytral declivity. Declivital striae without setae. Interstriae uniseriate. Smaller species, 1.8 mm long. Oriental Region . . . . *X. metagermanus* **(Schedl)** (Fig. 31)

32 (1) Margin of elytral declivity rounded or with a discontinuous row of small tubercules. Elytral disc with multiseriate interstrial punctures 33
Margin of elytral declivity serrate. Elytral disc with uniseriate interstrial punctures 36

33 (32) Margin of elytral declivity with a discontinuous row of small tubercles. Five striae visible on declivity. Smaller species, 2.3–2.4 mm long. Australian Region . . . . *X. woodi* **Dole and Beaver** (Fig. 44)
Margin of elytral declivity rounded. Six striae visible on declivity. Larger species 2.5–4.1 mm long. 34

34 (33) Basal pronotum lacking a dense patch of setae. Declivital striae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae multiseriate granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. 3.0–3.4 mm long. Australian Region . . . . *X. monteithi* **Dole and Beaver** (Fig. 33)
Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Declivital striae with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. 2.5–4.2 mm long 35

35 (34) Elytral surface shining. Prosternal intercoxal process shorter. Protibiae broadened toward apex, armed with 6 socketed teeth. Smaller species, 2.5–3.2 mm long. Australian Region. . . . . *X. rotundicollis* **(Browne) n. comb.** (Fig. 39)
Elytral surface duller. Prosternal intercoxal process taller, more pointed. Protibiae narrow; armed with 7 socketed teeth. Larger species, 3.5–4.2 mm long. Australian Region . . . . *X. russulus* **(Schedl) n. comb.** (Fig. 40)

36 (32) Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Body unicolorous. Six striae visible on elytral declivity. Striae granulate. Smaller species, 1.6–2.1 mm long 37

Basal pronotum lacking a dense patch of setae. Body bicolored, pronotum distinctly darker than elytra. Five striae visible on elytral declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae multiseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae. Larger species, 2.7–3.0 mm long. Oriental Region . . . . ***X. corthyloides* (Schedl)** (Fig. 15)

37 (36) Elytral disc gradually curving into declivity. Declivity shining. Declivital striae with appressed, hair-like setae, shorter than the width of second declivital interstriae. 1.9–2.1 mm long. Australian Region . . . . ***X. abruptulus* (Schedl)** (Fig. 6)

Declivital face steep and abruptly separated from disc. Declivity matte. Declivital striae with erect, acutely tapering, hair-like setae, shorter than the width of second declivital interstriae. 1.6–1.9 mm long. Australian Region . . . . ***X. queenslandi* Dole and Beaver** (Fig. 38)

38 (2) Declivital striae with a row of large, shallow punctures, arranged in a somewhat wavy line. Declivital interstriae shining, not densely granulate. Stouter species, 1.2–1.4 times as long as wide. Larger species, 2.9–3.3 mm long. Afrotropical Region and Oriental Region . . . . ***X. mancus* (Blandford)** (Fig. 28)

Declivital striae with smaller punctures arranged in perfectly straight rows. Declivital interstriae densely and finely granulate-punctate, giving the declivity a matte appearance. More elongate species, 2.5 times as long as wide. Smaller species, 2.7–2.9 mm long. Oriental Region . . . . ***X. amputatus* (Blandford) n. comb.** (Fig. 8)

TAXONOMY

Genus *Xylosandrus* Reitter

Xylosandrus Reitter 1913:80, 83. Type-species: *Xylosandrus morigerus* Blandford.

Apoxyleborus Wood 1980:90. Type-species: *Xyleborus mancus* Blandford, original designation. Synonymy: Wood 1984:229.

DIAGNOSIS.— *Xylosandrus sensu stricto* can be distinguished from other xyleborine genera by the following combination of characters: the stout body, usually about twice as long as wide, widely separated procoxae, flat scutellum that is flush with the surface of elytra, and obliquely truncate antennal club with the first segment forming a circular costa and dense pubescence on the oblique portion of the club.

***Xylosandrus abruptulus* (Schedl)**
Figure 6.

Xyleborus abruptulus Schedl, 1953:81. Lectotype ♀: Australia, Wongabel, 2 May 1941, A. R. Brimblecombe, from *Loranthus* sp.; NHMW; designated by Schedl, 1979a:9.

Xylosandrus abruptulus (Schedl): Schedl, 1964:213.

NOTES.— Schedl (1953) failed to designate a holotype in his original description of *X. abruptulus* and subsequently designated a lectotype (Schedl 1979a).

DIAGNOSIS.— Female 1.9–2.1 mm long; 2.1 times longer than wide. Body brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment 1 covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al.

2007). Pronotal vestiture of semi-appressed hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pornotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with seven or eight socketed teeth. Elytra 1.3 times longer than wide; 1.7 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margin with coarse serrations. Six straie visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital margins that are marked by coarse serrations: *X. abruptulus*, *X. corthyloides* (Fig. 15), and *X. queenslandi* (Fig. 38). *Xylosandrus abruptulus* can be distinguished from these species by the following characters: body unicolorous; basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium; elytral disc gradually curving into declivity; six striae visible on elytral declivity; and declivital striae punctate with appressed, hair-like setae, shorter than the width of second declivital interstriae.

DISTRIBUTION.— Australian Region: Australia (Queensland).

HOSTS. — *Loranthus* L. sp.

SPECIMENS EXAMINED.— (12 ♀; 0 ♂) TYPE MATERIAL: Lectotype *Xyleborus abruptulus* (♀; NHMW). Syntype: Australia, Wongabel, 2 May 1941, A.R. Brimblecombe, from *Loranthus* sp. (♀; BMNH).

OTHER MATERIAL: **Australian Region:** Queensland: N. Qld., Mt Finnigan Summit via Helenvale, 28-30 Nov 1985, G. Monteith and D. Cook, Pitfall traps, rainforest (1 ♀; RAB); N. QLD, Wallaman Falls Rd, 600 m, 14 Dec 1986–2 Jan 1987, Monteith, Thompson, and Hamlet, RF, Flight intercept trap (1 ♀; RAB); N. Qld., Mossman Bluff Track, 5-10 km W Mossman, Site 9, 1260 m, 1-17 Jan 1989, Monteith, Thompson, and ANZSES, flt. intercept (2 ♀; RAB); N. Qld., Mossman Bluff Track, 5-10 km W Mossman, Site 7, 7100 m, 20 Dec 1989–15 Jan 1990, Monteith, Thompson, and ANZSES, flt. intercept (1 ♀; RAB); N.E. QLD, Cardwell Range, Upper Broadwater Ck Valley, 750 m, 17-20 Dec 1986, Monteith, Thompson, and Hamlet, Flight intercept trap (1 ♀; RAB); NEQ: 17º26'S, 145º42'E, Hughes Road, Topaz, 650 m, 6 Dec 1993–25 Feb 1994, Monteith, Cook, Janetzki, RF Pitfalls (1 ♀; RAB); NEQ: 16º24'S x 145°17'E, Upper High Falls Ck., 1000 m, 25 Jan–12 Feb 1996, R. Wertz, Flight intercept trap (1 ♀; RAB); N. E. Qld, Kirrama Range, (Douglass Ck Rd, 800 m), 10 Dec 1986–11 Jan 1987, Monteith, Thompson, and Hamlet, RF, Flight intercept trap (2 ♀; RAB).

Xylosandrus adherescens Schedl

Figure 7.

Xylosandrus adherescens Schedl, 1971:375. Holotype ♀: Hui (?), Chuo Chan [Vietnam], Nov. 03; NHMW.

DIAGNOSIS.— Female 2.0 mm long; 2.0 times longer than wide. Body light brown to brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately puncatate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined with. Elytra 1.3 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity.

Declivity convex, lateral margin carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. eupatorii* (Fig. 22) and *X. germanus* (Fig. 24). These three species share the following characters: elytral disc gradually curving into declivity; pronotum with a lateral carina; interstriae on elytral disc uniseriate punctate; and declivital striae with semi-appressed, hair-like setae, shorter than the width of the second declivital interstriae. *Xylosandrus adherescens* can be distinguished from these species by the following characters: pronotum wider than long; pronotal disc glabrous, except for a dense patch of short, erect setae basally, indicating the presence of a pronotal-mesonotal mycangium; and declivital interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

DISTRIBUTION.— **Oriental Region:** Vietnam.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (1 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xylosandrus adherescens* (♀; NHMW).

Xylosandrus amputatus (Blandford), new combination

Figure 8.

Xyleborus amputatus Blandford, 1894b:575. Holotype ♀: Japan: Higo; BMNH.
Amasa amputatus (Blandford): Wood and Bright, 1992:682.

NOTES.— This species was first included in *Amasa* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DIAGNOSIS.— Female 2.7–2.9 mm long; 2.5 times longer than wide. Body light brown to brown; declivity distinctly darker than rest of elytra; legs and antennae the same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separted. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibiae with 11 socketed teeth. Elytra 1.3 times longer than wide; 2.3–2.4 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity concave, lateral margins carinate, with carina extending beyond 7th interstriae, forming a circumdeclivital ring. Four striae visible on declivity. Striae punctate, without setae. Interstriae finely granulate-punctate, without setae.

This species is one of two *Xylosandrus* with the margin of the elytral declivity with a carina that extends beyond the 7th interstriae, forming a circumdeclivital ring: *X. amputatus* and *X. mancus* (Fig. 28). *Xylosandrus amputatus* can be distinguished from *X. mancus* by the following characters: 2.5 times as long as wide; declivity without setae; declivital striae with smaller punctures arranged in perfectly straight rows; and declivital interstriae densely and finely granulate-punctate, giving the declivity a matte appearance.

DISTRIBUTION.— **Oriental Region:** China, Japan, Taiwan.

HOSTS.— *Acer* L. sp., *Cinnamomum mairei* H. Lév., *Cinnamomum* L. sp., *Machilus* Nees sp., *Pelargonium hortorum* L. H. Bailey, *Ziziphus jujuba* Lam.

Specimens examined.— (3 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** China Gang-keu, SW. Fukien, S. China, VII-26-36, L. Gressit Collection (1 Homotype ♀; USNM); Japan: Okinawa Id, June 23, 1945, F.N. Young, No 54 (1 ♀; USNM); Japan: Kagoshima Pref., Tarumizu Oonohara, Broadleaf forest, 425 m, 14 Aug 2000, Yoshikazu Sato Coll., Ex; ETOH-baited trap (1 ♀; USNM).

Xylosandrus arquatus (Sampson)

Figure 9.

Xyleborus arquatus Sampson, 1912:246. Holotype ♀: Ceylon [Sri Lanka]; BMNH.
Xylosandrus arquatus (Sampson): Schedl, 1964:213.

Diagnosis.— Female 2.3–2.5 mm long; 2.3 times longer than wide. Pronotum distinctly lighter than elytra; pronotum light brown and elytra black; antennae and legs light brown. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum basic (type 2, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Base of pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately granulate. Pronotum moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 8 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.4 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae punctate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus*, *X. discolor* (Fig. 20), *X. ferinus* (Fig. 23), and *X. mesuae* (Fig. 30). *Xylosandrus arquatus* can be distinguished from *X. discolor* by the following characters: elytral disc gradually curving into declivity. *Xylosandrus arquatus* can be distinguished from *X. ferinus* and *X. mesuae* by the following characters: 2.3–2.5 mm long; pronotum light brown and elytra black; six striae visible on elytral declivity; declivital striae with erect, hair-like setae; and declivital interstriae punctate.

Distribution.— **Oriental Region:** Sri Lanka.

Hosts.— *Cinnamomum* L. spp., "*Kududavula* sp." (Sri Lanka), *Symplocos loha* Buch.-Ham. ex D. Don.

Specimens examined.— (29 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** Sri Lanka: Ceylon [Sri Lanka] (1 ♀; NHMW); Sri Lanka: Bad. Dist., Pattopola, 200 mtrs., 3 June 1975, S.L. Wood, *Kududavula* sp. (2 ♀; USNM); Sri Lanka: Mat. Dist., Enselwatte, 800 mtrs., 25 May 1975. S.L. Wood, misc. hosts (1 ♀; USNM); Sri Lanka: N. E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S.L. Wood, collected from branches (1 ♀; USNM); Sri Lanka: N. E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S.L. Wood. Host: *Symplocos loha* (18 ♀; USNM); Sri Lanka: N.E. Dist., 11 km SE Nuara Eliya, 1 June 1975, 2000 m. S.L. Wood, collected from twigs (6 ♀; USNM).

Xylosandrus assequens Schedl

Figure 10.

Xylosandrus assequens Schedl, 1971:376. Holotype ♀: Malaya, Kelantan, Bukit Kabong, 14.ii.1947, in *Xanthophyllum* sp., F.G. Browne.; BMNH.

Diagnosis.— Female 1.6–2.3 mm long; 2.0 times longer than wide. Body brown to dark brown; antennae and legs light brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Pronotum punctate basally; lacking a dense patch of setae. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 9 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.3 times longer than wide; 1.7 times longer than pronotum. Discal striae punctate; interstriae multiseriate puncate; striae and interstriae confused on disc. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. deruptulus* (Fig. 19). *Xylosandrus assequens* can be distinguished from *X. deruptulus* by the following characters: 2.0 times longer than wide; elytra of equal length and width; elytral disc with interstriae densely punctured; declivital interstriae multiseriate; and declivital surface matte in appearance.

Distribution.— **Oriental Region:** Brunei, Malaysia.

Hosts.— *Xanthophyllum* Roxb. sp.

Specimens examined.— (2♀; 0 ♂) Type material: Holotype *Xylosandrus assequens* (♀; BMNH).

Other material: **Oriental Region:** Malaysia: Malaysia: Sabah Sipitang, Mendolong, T6/R, 31.iii.1989, leg. S. Abdebratt (1 ♀; RAB).

Xylosandrus beesoni Saha, Maiti, and Chakraborti

Illustrated in Saha et al. 1992.

Xylosandrus beesoni Saha, Maiti, and Chakraborti, 1992:11. Holotype ♀: India: Rangirum (1846 m), Darjiling Dist., coll. J.C.M. Gardner, 8.ix.1929, ex. "*Symplocos theaefolia*" [*Symplocos theifolia*].

Diagnosis.— Female 2.8–2.9 mm long; 2.0 times as long as wide. Body yellowish brown. Frons reticulate. Antennae with 5 funicular segements. Antennal club obliquely truncate; frist segment forming a circular costa; segment one covering entire posterior face. Pronotum wider than long. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibiae with 8 socketed teeth. Elytra longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytral steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity with striae 4 and 5 forming a loop. Striae granulate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with a single row of long hair-like setae along with a dense vestiture of shorter appressed setae.

This species is morphologically similar to *X. discolor* (Fig. 20), *X. jaintianus* (Fig. 27), and

X. subsimiliformis (Fig. 41). *Xylosandrus beesoni* can be distinguished from these species by the following characters: declivital face covex, five striae visible on declivity with striae 4 and 5 forming a loop, and declivital interstriae with a single row of long, erect, hair-like setae, along with a dense vestiture of shorter appressed setae.

DISTRIBUTION.— **Oriental Region:** India.

HOSTS.— *Symplocos theifolia* D. Don.

SPECIMENS EXAMINED.— (0 ♀; 0 ♂) TYPE MATERIAL: Unable to examine type material.

DISCUSSION.— This species was described by Saha, Maiti, and Chakraborti (1992) from four female specimens from a single collecting event. All specimens are deposited in collections in India (FRI and ZSI) and were not available for examination as part of this revision. However, based on the original species description and corresponding images, *X. beesoni* is clearly a member of the *Xylosandrus senso stricto* group. The species description was also detailed enough to be used to score morophological characters for the phylogenetic analysis.

Xylosandrus borealis Nobuchi

Figure 11.

Xylosandrus borealis Nobuchi, 1981:34. Holotype ♀: Honshu, Kyushu (Japan); Nobuchi Collection, Ibaraki, Japan.

DIAGNOSIS.— Female 2.0–2.1 mm long; 1.8–1.9 times as long as wide. Body yellowish brown to light brown; antennae and legs the same color as body. Frons rugose with a distinct median keel. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 1.1 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size. Lateral aspect of pronotum prolonged anteriorly (type 9, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 8 socketed teeth. Elytra 1.0–1.3 times longer than wide; 1.1 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytral steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with a vestiture of appressed, hair-like setae, shorter than the width of second declivital interstriae with an interspersed row of long, erect, hair-like setae.

This species is morpholocially similar to *X. brevis* (Fig. 13). *Xylosandrus borealis* can be distinguished from *X. brevis* by the matte appearance of its elytral declivity, due to dense and closely placed interstrial granules, and by its smaller size of 2.0–2.1 mm.

DISTRIBUTION.— **Oriental Region:** Japan. **Palearctic Region:** Korea.

HOSTS.— *Camellia sasanqua* Thunb., *Styrax obassia* Siebold and Zucc.

SPECIMENS EXAMINED.— (4 ♀; 0 ♂) TYPE MATERIAL: Unable to examine type material.

OTHER MATERIAL: **Oriental Region**: Japan: Okusa, Japan, 20.VII.1935, Coll. K. Baba (4 ♀; USNM).

Xylosandrus borneensis Dole and Cognato, sp. nov.

Figure 12.

Description.— Female (Fig. 12): 1.5–1.6 mm long, 2.1 times longer than wide, with pronotum yellowish brown, slightly darker toward apex, elytra brown, ventral side and appendages yellowish brown. Frons convex, shining, coriaceous, punctate between eyes, with deep, vertically elongate punctures, a single hair-like seta originating from each puncture. Epistoma with row of short hair-like setae along lower margin. Eyes emarginate. Antennal funicle 5-segmented, scape and funicle with sparse, short, hair-like setae; club obliquely truncate, first segment sclerotized, forming a circular costa (type 1, Hulcr et al. 2007), circular costa closed anteriad, oblique part of club densely pubescent, second segment not corneous; posterior face of club covered entirely by first segment (type 1, Hulcr et al. 2007). Pronotum 0.9 times longer than wide, basic shape dorsally (type 2, Hulcr et al. 2007), widest about two-thirds pronotal length from base, anterior third broadly rounded toward apex, basal angles rounded, anterior margin with 8-10 asperities; anterior slope asperate, asperities smallest at summit and increasing in size toward anterior margin; disc moderately punctate, patch of denser punctures medially at base, hair-like setae originating from punctures, background sculpture finely granulate; lateral aspect of pronotum basic (type 0, Hulcr et al. 2007), lateral costa extending two-thirds pronotal length, lateral carina present only in basal ¼ of prontum; pronotal vestiture of short, semi-appressed, hair-like setae. Scutellum triangular, flush with surface of elytra. Elytra 1.1 times longer than wide, 1.1 times as long as pronotum, parallel-sided on basal two-thirds and then broadly rounded toward apex; disc shining; declivity matte in appearance. Striae impressed beginning slightly before declivital origin and becoming more deeply impressed on declivity, shallowly and regularly punctate, punctures becoming less distinct on declivity, with very short, appressed setae originating from punctures. Interstriae equal the width of striae, finely granulate, giving a matte appearance, short (less than or equal to width of interstria), erect, hair-like setae in uniseriate rows; interstriae 4–6 not reaching apex of the declivity. Declivity commencing behind mid-point of elytra, abruptly and steeply separated from disc; lateral margins carinate to 7th interstriae. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 7–8 socketed teeth; metatibiae with 8–9 socketed teeth. Abdominal ventrites evenly punctured, punctures with short and long, moderately appressed, hair-like setae.

Specimens examined.— (11 ♀; 0 ♂) Type material: Holotype ♀: Malaysia, Sabah, Danum Valley, 120 m asl. July 2006 Hulcr coll. Burseraceae, twig. Vial 1694. In MSU. *Paratypes* ♀: Malaysia, Sabah, Danum Valley, 120 m asl. July 2006 Hulcr coll. Burseraceae, twig. Vial 1694. One paratype in FRCS. Nine paratypes in MSU. One paratype female was used for DNA extraction and its remains are vouchered in MSU. Brunei [Darussalam]: Temburong: nr. K[uala] Belalong Field Stud[ies]. Centre, 4°33'N 115°09'E, 150m, 21.ii.1992 (R.A.Beaver). One paratype in RAB. Malaysia: Sabah, Sipitang, Mendolong, 11.v.1988 (2); 10.iii.1989 (1); 14.iii.1989 (2) (S.Adebratt).Three paratypes in MZLU; two in RAB.

Male: Unknown

Etymology.— This species is named *borneensis* after the type locality.

Diagnosis.— This species can be distinguished from all other known *Xylosandrus* by the deeply impressed declivital striae, which form six distinct ridges on the declivity. It is morphologically similar to *X. pygmaeus* (Fig. 38). *Xylosandrus borneensis* can be distinguished from *X. pygmaeus* by the following characters: pronotum without lateral carina; declivital striae more deeply impressed; six striae visible on elytral declivity; declivital striae without setae; and declivital interstriae finely granulate, giving the declivital face a matte appearance, with erect, hair-like setae, shorter than the width of second declivital interstriae.

Distribution.— **Oriental Region:** Malaysia (Sabah).

Hosts.— Burseraceae.

Discussion.— This species was found in association with the mycocleptic species *Diuncus mucronatulus* (Eggers) (Hulcr 2009).

Xylosandrus brevis (Eichhoff)

Figure 13.

Xyleborus brevis Eichhoff, 1877:121. Syntypes ♀: Nipon (Hagi Hiller) and Nipon Insula Asiatica; IRSNB.
Xylosandrus brevis (Eichhoff): Browne, 1965:204.
Xyleborus cucullatus Blandford, 1894c:121. Syntypes ♀: Kurigahara, and Konose in Higo, Japan; BMNH. Synonymy: Murayama, 1954:176.

Diagnosis.— Female 2.5–2.8 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons rugose, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of dense, semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by a distance less than or equal to their size. Lateral aspect of pronotum prolonged anteriorly (type 9, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 10–11 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. borealis* (Fig. 11). *Xylosandrus brevis* can be distinguished from *X. borealis* by the shining appearance of its elytral declivity and by its larger size of 2.5–2.8 mm.

Distribution.— **Oriental Region:** Japan, Taiwan, Thailand. **Palearctic Region:** China (Xizang [Tibet]), Korea, Nepal.

Hosts.— *Berberis* L. sp., *Camellia japonica* L., *C. sasanqua* Thunb., *Cinnamomum japonicum* Siebold, *Diospyros kaki* Thunb., *Fagus crenata* Blume, *Grevillea* Knight sp., *Hamamelis* L. sp., *Lindera* Thumb. spp., *Machilus japonica* Siebold and Zucc., *Machilus thunbergii* Siebold and Zucc., *Maesa tenera* Mez, *Meliosma cuneifolia* Franch., *Parabenzoin praecox* Nakai, *Quercus* L. spp., *Smilax china* L., *Styrax obassia* Siebold and Zucc., *Viburnum* L. sp., *Weigela hortensis* C. A. Mey.

Specimens examined.— (25 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** Japan: Japan: Kagoshima Pref., Tarumizu Oonohara, Broadleaf forest, 425 m, 14 May 2001, Yoshikazu Sato Coll. Ex; ETOH-baited trap (4 ♀; MSU); Japan, Ookusa, 20.VI.1933. Coll. K. Baba (3 ♀; USNM); Japan: Ryukyus, Mt. Yonaha-dake, Okinawa-honto Is., 5.VI.1997, H. Goto leg., Host tree: *Machilus japonica* Sieb. & Zucc. (4 ♀; RAB); Japan, Tamagowa, 29.VII.1980, *Fagus crenatus* (3 ♀; USNM); Japan, Tokyo, Takao, VII.31.1957, Coll. A. Nobuchi (4 ♀; USNM). Taiwan: Taiwan: Taichung, Hsien: Shei-Pa N.P., 10.5.2004, J-T. Yang, Pitfall (5 ♀; RAB). **Palearctic Region:** Nepal: Nepal: Sikha 83°40′E, 28°26′N, 8000 ft. 24–26.v.1954. K.H. Hyatt. Litter in oak forest (2 ♀; BMNH).

***Xylosandrus compactus* (Eichhoff)**
Figure 14.

Xyleborus compactus Eichhoff, 1875:201. Syntypes 2 ♀, 1 ♂: Japan; NHMW (syntypes in Hamburg Museum lost).
Xylosandrus compactus (Eichhoff): Nunberg, 1959:434.
Xyleborus morstatti Hagedorn, 1912:37. Syntypes ♀: Amani, Deutsch-Ostafrika; Hamburg Museum, lost.
Xylosandrus morstatti (Hagedorn): Browne, 1963:55. Synonymy: Murayama and Kalshoven, 1962:247.

DIAGNOSIS.— Female 1.4–1.9 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed hair-like setae; setae less dense on disc. Basal pronotun with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 7 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.3 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae punctate-granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. curtulus* (Fig. 17) and *X. pusillus* (Fig. 36). It can be distinguished from *X. curtulus* by a pronotal disc that is evenly pubescent, rather than mostly glabrous. *Xylosandrus compactus* is nearly morphologically identical to *X. pusillus*. The only character distinguishing the two species is the degree of body stoutness, with *X. compactus* being 2.3 times as long as wide and *X. pusillus* being 1.9 times as long as wide. However, this is too large a disparity to warrant synonymizing the two species without further investigation.

DISTRIBUTION.— **Afrotropical Region:** Cameroon, Cameroon Islands (Grande Comoro), Equatorial Guinea, Fernando Poo, Gabon, Ghana, Ivory Coast, Liberia, Madagascar, Mauritania, Nigeria, Reunion Islands, Senegal, Seychelles Islands, Sierra Leone, South Africa, Tanzania, Uganda. **Nearctic Region (Introduced)** United States (Alabama, Florida, Louisiana, Mississippi North Carolina, East Texas). **Neotropical Region:** Brazil, Cuba, Peru, Peutro Rico, Virgin Islands. **Oceania:** Hawaiian Islands (Hawaii, Kauai, Lanai, Maui, Molokai, Oahu), Samoan Islands. **Oriental Region:** China (Guangdong), India (Tamil Nadu), Indonesia (Java), Japan (Mainland, Bonin Islands, Ryukyu Islands), Malaysian Peninsula, Malaysia (Sabah), Philippines, Sri Lanka, Taiwan, Thailand, Vietnam.

HOSTS.— *Acacia mangium* Willd., *Acalypha* L. sp., *Acer* L. sp., *Acrocarpus fraxinifolius* Wight and Arn., *Adenanthera pavonina* L., *Albizia chinensis* Merr., *A. lebbeck* Benth., *A. zygia* (DC.) Macbride, *Ardisia paniculata* Roxb., *Aucoumea klaineana* Pierre, "Bamboo Orchid" (Hawaii), *Bauhinia* L. sp., *B. tomentosa* L., *Bombax malabaricum* DC., *Cajanus cajan* (L.) Millsp., *Camellia sinensis* Kuntze, *Cassia hirta* Wild., *C. mutijuga* Rich., *C. siamea* Lam., *C. tora* L., *Cattleya* Lindl. sp., *Cinnamomum camphora* (L.) J. Presl, *C. iners* Reinw., *C. zeylanicum* Broyn., *Clerodendron* Burm. sp., *Coffea* L. sp., *C. arabica* L., *C. bukobensis* Zimmermann, *C. canephora* Pierre., *C. liberica* Bull., *C. quillon* Wester, *C. robusta* L. Lind., *C. stenophylla* G. Don., *Cola nitida* (Vent.) Schott and End., *Crotalaria* L. sp., *Cryptocarya* Gay sp., *Dendrobium* Sw. sp., *D. pha-*

laenopsis Fitz., *D. veratrifolium* Lindl., *Desmodium ovalifolium* Guill., *Drypetes phyllanthoides* (Rock) Sherff, *Elaeis guineensis* Jacq., "Elderberry" (Singapore), *Entandrophragma utile* Sprague, *Erythroxylon novagranatense* Hieron., *Eupatorium pallescens* DC., *Eusideroxylon zwageri* Teijsm., *Ficus aurea* Nutt., *F. soroceoides* Bar., *Gossypium* L. sp., *Haasia* Nees. sp., *Hopea parviflora* Bedd., *Ichthyomethia communis* S. F. Blake, *Indigofera suffruticosa* Mill., *Jacobinia* Moric. sp., *Khaya grandifoliola* C. DC., *K. senegalensis* A. Juss., *Leucaena glauca* Benth., *Litsea cassiaefolia* Blume, *Mangifera indica* L., *M. odorata* Griff., *Melia azedarach* L., *Muntingia calabura* L., *Myrciaria dubia* (H. B. and K.) McVaugh, *Nectandra angustifolia* Nees. and Mart., *Olea europaea* L., *Persea* Mill. sp., *Persea americana* Miller, *P. gratissima* Gaertn., *P. indica* Sprang., "*Prosopis nudiflora*" (Java: Schedl 1963a), Quercus *myrsinaefolia* Blume, *Rhizophora* L. sp., *Sambucus* L. sp., *S. canadensis* L., *S. javanica* Reinw., *Shorea* Roxb. ex. C. F. Gaertn. sp., *S. sumatrana* (Slooten) Desch., *Spathodea campanulata* P. Beauv., *Swietenia macrophylla* King, *S. mahagoni* Jack., *Tephrosia maxima* Pres., *Thea sinensis* L., *Theobroma cacao* L., *Toona sureni* Merr., *Turraeanthus africana* Pellegr., *Vanda coerula* Griff., *V. teres* Lindl., *V. tricolor* Lindl., *Vitex* L. sp., "Wild Grape" (Florida).

SPECIMENS EXAMINED.— (123 ♀; 8 ♂) TYPE MATERIAL: Syntypes *Xyleborus compactus* (2 ♀, 1 ♂; NHMW).

OTHER MATERIAL: **Afrotropical Region:** Ghana: Ghana: Kumasi, 12.9.61 (6 ♀, 1 ♂; USNM). Madagascar: Madagascar: Prov. Flanarantsoa, 7 km W Ranomafana, 1100 m, 1-7 November 1988, W. E. Steiner (1 ♀; USNM). **Nearctic Region:** United States: Florida: Dade Co. Coral Gables, Matheson Hammock Pk., 27 June 1980, O'Brien and Wibmer (1 ♀; CAS); Florida: Key Largo, 6.25.1951, Price Beamers–Wood, *Ichthyomethia communis* (1 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers–Wood (4 ♀, 1 ♂; USNM); Florida: Key Largo, 6.25.1951, Price Beamers–Wood, taken on wild grape (7 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers–Wood, *Ardisia paniculata* (4 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers–Wood, *Cajanus cajan* (6 ♀; USNM); Florida: Key Largo, 6.25.1951, Price Beamers–Wood, taken on *Ficus aurea* (1 ♀; USNM); Florida: Tallahassee, Fall, 1979, C. W. O'Brien, reared ex dogwood flags, emer. Sum 1980 (23 ♀; CAS); Florida, W. Palm Beach, I.27.61 (6♀; USNM). **Neotropical Region:** Peru: Perou-Loreto, Iquitos, Juin 1990, G. Couturier Col., Plante–Hôte, *Myrciaria dubia* (1 ♀; USNM). Puerto Rico: Puerto Rico: Carite St. For., VII.28.1999, C.W.O'Brien, P. Kovarik (1 ♀; CAS). **Oceania:** Hawaiian Islands: Hawaii: Mt. Puu Puae, Waianae Mts., Cahu 425 m., in twigs of *Drypetes phyllanthrides*, 1.VII.1970. W.C. Gagne Collector (1 ♀; NHMW); Hawaii: Oahu, Kailua, I. 1962, Ex *Vitex* sp. (10 ♀; CAS); Hawaii: Oahu, Kailua, I.2.62., ex. *Vitex* sp. Roy Hirata Coll. (2 ♀, 3 ♂; USNM); Hawaii: Oahu, Nuuanu, May 8, 1931, H.L. Lyon, Elderberry stems imported from Singapore (1♀; USNM); USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21°25'N, 157°51'W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest, A. Newton and M. Thayer, #869, window trap (4 ♀; FMNH); Quarantine from Hawaii at Carpenteria, California, VI.20.2001, Ex. Bamboo Orchid (2 ♀; CSCA). **Oriental Region:** India: India: Coffee Research Station, Chilemagalur dist., Mysore, 2.I.1966 (7 ♀; CAS); South India: Nilgiri Hills, Devala, 3200 ft., XI.60, P. S. Nathan (23 ♀; 2 ♂; USNM). Indonesia: Java: Boger, VIII.1964, N.L.H. Krauss, Coffee (1 ♀; USNM); E. Java, Ma Lang, 10.1951, Planta nutrix, Coffea (4 ♀; USNM). Sri Lanka: Sri Lanka: Col. Dist., Labugama, 23 June 1975, S.L. Wood, collected from branches (1 ♀; USNM).

Xylosandrus corthyloides (Schedl)

Figure 15.

Xyleborus corthyloides Schedl, 1934:86. Lectotype ♀: Java, Mount Gede, 800 m, ex Zingiberaceae; NHMW; designated by Schedl, 1979a:66.

Xylosandrus corthyloides (Schedl): Wood and Bright, 1992:790.

Xyleborus percorthyloides Schedl, 1957:85. Lectotype ♀: Java, Mount Gede, 800 m; NHMW; designated by Schedl, 1979a:66. Synonymy: Wood and Bright, 1992:790.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination." *Xyleborus percorthyloides* was also listed as a synonym (an "unneeded replacement of *corthyloides*") by Wood and Bright (1992), but was not indicated as a "new synonymy."

DIAGNOSIS.— Female 2.7–3.0 mm long; 2.1 times longer than wide. Body bicolored, pronotum distinctly darker than elytra; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Lacking a dense patch of setae at base of pronotum. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibial teeth not visible on specimens examined; metatibiae with 10 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins with small serrations. Five striae visible on declivity. Striae punctate, with erect, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital margins that are marked by coarse serrations: *X. abruptulus* (Fig. 6), *X. corthyloides*, and *X. queenslandi* (Fig. 38). *Xylosandrus corthyloides* can be distinguished from these species by the following characters: 2.7–3.0 mm long; basal pronotum lacking a dense patch of setae; body bicolored, pronotum distinctly darker than elytra; five striae visible on elytral declivity; and declivital striae punctate.

DISTRIBUTION.— **Oriental Region:** Indonesia (Java).

HOSTS.— Zingiberaceae.

SPECIMENS EXAMINED.— (2 ♀; 1 ♂) TYPE MATERIAL: Holotype *Xyleborus corthyloides* (♀; NHMW). Paratype *Xyleborus percorthyloides* Java: Mt. Gede, 14-IX-1922, 800 m, L.G.E. Kalshoven, Zingiberaceae (♀; NHMW). Allotype *Xyleborus percorthyloides* Java: Mt. Gede, 14-IX-1922, 800 m, L.G.E. Kalshoven , Zingiberaceae (♂; NHMW).

***Xylosandrus crassiusculus* (Motschulsky)**

Figure 16.

Phlaeotrogus crassiusculus Motschulsky, 1866:403. Syntypes ♀: published as Des Montagnes de Nura-Ellia, Ceylon types labeled India Occidentale; IZM.

Xylosandrus crassiusculus (Motschulsky): Wood, 1982:766.

Xyleborus semiopacus Eichhoff, 1878:334. Syntypes ♀: Nipon insula Japonica; Hamburg Museum, lost. Synonymy: Wood, 1969:119.

Xyleborus semigranosus Blandford, 18 96a:211. Holotype ♀: Sumatra; BMNH. Synonymy: Schedl 1959:496.

Xyleborus ebriosus Niisima, 1909:154. Holotype ♀: Sapporo, Japan; Nobuchi Collection, Ibaraki. Synonymy: Choo, 1983:98.

Dryocoetes bengalensis Stebbing, 1908:12. Syntypes ♀: Goalpara, Assam; FRI. Synonymy: Beeson, 1915:297.

Xyleborus mascarenus Hagedorn, 1908:379. Syntypes ♀: Mauritius, and Bomole et Amani in Deutsch-Ostafrika; NHMW (syntypes in Hamburg Museum lost). Synonymy: Eggers, 1923:130.

Xyleborus okoumeensis Schedl, 1935:271. Syntypes ♀: imported Okoume logs, Carlshafen, Hessen-Nassau [Germany]; NHMW. Synonymy: Schedl, 1959:496.

Xyleborus declivigranulatus Schedl, 1936:30. Lectotype ♀: Selangor, Malay Peninsula; NHMW; designated by Schedl, 1979a:76. Synonymy: Schedl, 1959:496.

Diagnosis.— Female 1.7–2.9 mm long; 2.2 times longer than wide. Body light to dark brown; antennae and legs yellowish brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely punctate, with punctures separated by a distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated, though less so than in most *Xylosandrus* species. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 14–16 socketed teeth. Elytra 1.2 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Six striae visible on declivity. Striae granulate, with erect, hair-like setae, shorter than twice the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. hirsutipennis* (Fig. 25). Both species have a declivital face that is matte in appearance due to densely, finely, and confusedly granulate striae and interstriae. *Xylosandrus crassiusculus* can be distinguished from *X. hirsutipennis* by the following characters: frons rugose; pronotum without a lateral carina; elytral disc multiseriate punctate; six striae visible on the elytral declivity; declivital striae with erect, hair-like setae shorter than the width of second declivtial interstriae; and declivital interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

Distribution.— **Afrotropical Region:** Cameroon, Congo, Equatorial Guinea, Fernando Poo, Gabon, Ghana, Ivory Coast, Kenya, Madagascar, Mauritania, Nigeria, Sierra Leone, Seychelles Islands, Tanzania, Zaire. **Australian Region:** New Guinea. **Nearctic Region (Introduced):** United States (Alabama, Delaware, Florida, Georgia, Kansas, Louisiana, Maryland, Mississippi, North Carolina, Oregon, South Carolina, Tennessee, Texas). **Neotropical Region:** Costa Rica, Panama. **Oceania:** Hawaiian Islands (Hawaii, Kauai, Maui, Oahu), Micronesia (Palau Islands), New Caledonia, Samoan Islands. **Oriental Region:** Burma, Hong Kong (Fujian), China (Hunan, Sichuan), India (Andaman Islands, Assam, Bengal, Himachal Pradesh, Madhya Pradesh, Maharashtra, Tamil Nadu, Uttar Pradesh), Indonesia (Borneo, Celebes, Java, Sumatra), Japan (Mainland, Bonin Islands), Malaysian Peninsula (Sabah, Sarawak), Philippines, Sri Lanka, Taiwan, Thailand, Vietnam. **Palearctic Region:** Bhutan, China (Xizang [Tibet]), Germany [Imported], Korea, Nepal.

Hosts.— *Acacia* Mill. sp., *A. decurrens* Willd., *A. mangium* Willd., *Acrocarpus* J.R. Forst and G. Forst spp., *Adina rubescens* Hemsl., *Adinandra dumosa* Jack., *Adinobotrys atropurpureus* Dunn., *Afzelia bipindensis* Harms, *Agathis* Salisb. sp., *Albizia* Durazz. sp., *A. chinensis* Merr., *A. ferruginea* Benth., *A. gummifera* (Gmel.) C.A. Sm., *A. lebbek* L., *A. moluccana* Miq., *A. stipilata* Boivin, *A. zygia* (DC.) Macbride, *Alnus* Mill. sp., *Alstonia* R. Br. sp., *Altingia excelsa* Nor., *Amoora* Roxb. sp., *Angylocalyx pynaertii* De Wild., *Anisoptera* Korth. sp., *Anthonota fragrans* Baker, *Antiaris africana* Engl., *Antrocaryon micraster* A. Chev. and Guill., *Artocarpus* J.R. Forst. and G. Forst. sp., *A. chaplasha* Roxb., *Aucoumea klaineana* Pierre, *Barteria nigritiana* Hook., *Bauhinia tomentosa* L., *Bischofia javanica* Blume, *Buchanania arborescens* Blume, *B. sessilifolia* Blume, *Cacao* Mill. sp., *Calamus* L. sp., *Calophyllum tetrapterum* Miq., *Camellia sinensis* (L.) O. Kuntze., *C. thea* Link., *Canarium* L. sp., *Cannabis sativa* L., *Carapa procera* DC., *Carica papaya* L., *Carya illinoinensis* (Wangenh.) Koch, *Caryota* L. sp., *Castanea argentea* Bl., *C. javanica* Blume, *Castanopsis* (D. Don) Spach spp., *Castilla elastica* Cerv., *Casuarina equisetifolia* L., *Cecropia* L. leaf petiole, *Cedrela toona* Roxb. ex Rottler and Willd., *Ceiba pentandra* Gaertn., *C. thonningii* A. Chev., *Celtis brownii* Rendl., *C. luzonicus* Warb., *C. mildbraedii* Engl., *C. zenkeri* Engl., *Chlorophora excelsa* Benth. and Hook., *Chloroxylon swietenia* DC., *Chrysophyllum* L. sp., *Cinchona* L. sp., *Cinnamomum camphora* (L.) J. Presl, *Cinnamomum* L. sp., *Cistanthera* K. Schum. sp., *Cleistopholis patens* Benth., *Coelocaryon preussii* Warb., *Coffea* L. sp., *C. robusta* L. Linden, *Cylicodiscus gabunensis* Harms, *Cynometra hankie* Harms, *Dacryodes pubescens* (Vermoesen) H.J. Lam., *Dactylocladus stenostachya* Oliv., *Dalbergia latifolia* Roxb., *D. sissoo* Roxb., *Dialium corbisieri* Staner, *D. pachyphyllum* Harms, *Dillenia pentagyna* Roxb., *Dimocarpus longan* Lour., *Dipterocarpus* C.F. Gaertn. spp., *D. baudii* Korth., *Distemonanthus benthamianus* Baill., *Doona zeylanica* Thwaites., *Dryobalanops* C.F. Gaertn. sp., *Drypetes leonensis* Pax. Var. *glabra* J. Léonard, *Elaeis guineensis* Jacq. (leafstalks), *Elaeocarpus sericeus* Stapf., "*Elaeocarpus tetrapterum*" (Wood and Bright 1992), *E. tuberculatus* Roxb., *Entandrophragma angolense* C. DC., *E. cylindricum* Sprague, *E. utile* Sprague, *Erythrina* L. spp., *E. lithosperma* Miq. var. *inermis* Kds. and Val., *Erythrophleum guineense* G. Don, *Eucalyptus deglupta* Blume, *Eucalyptus* L'Hér. sp., *E. robusta* Sm., *Eugenia caryophylla* St. Lag., *E. jambolana* Lam., *Eupatorium pallescens* DC., *Fagara macrophylla* (Oliv.) Engl., *Fagus crenata* Blume, *Ficus* L. spp., *Garcinia polyantha* Oliv., *G. punctata* Oliv., *Gliricidia maculate* H.B. and K., *Gluta tourtour* Marchand, *G. travancorica* Bedd., *Gmelina arborea* Roxb., *Gossweilerondendron balsamiferum* Harms, *Grevillea* Knight sp., *G. robusta* A. Cunn., *Guarea cedrata* A. Chev., *G. laurentii* De Wild., *Hannoa klaineana* Pierre, *Haronga paniculata* (Pert.) Lodd., *Hevea brasiliensis* (Willd. ex A. Juss) Müll. Arq., *Holigarna arnottiana* Hook., *Hopea beccariana* Burck, *H. ferrea* Heim, *H. odorata* Roxb., *H. parviflora* Bedd., *H. wightiana* Wall., "*Ilteocafus baudii*" [?] (China), *Julbernardia sereti* (De Wild.), *Khaya ivorensis* A. Chev., *Kayea floribunda* Wall., *Koompassia malaccensis* Maingay, *Lagerstroemia flos-reginae* Retz., *L. speciosa* Pres., *Lannea grandis* Enql., *Lasiococca* Hook. sp., Lauraceae sp., *Lecanodiscus cupanoides* Planch., *Leea crispa* L., *L. sambucina* (L.) Willd., "Liana" [woody vine] (Sri Lanka), *Lithocarpus wallichiana* Rehder, *Lophira procera* A. Chev., *Lovoa klaineana* Pierre, *L. trichiliodes* Harms, *Luffa* Mill. sp., *Macaranga monandra* Müll.-Arg., *Machilus odoratissima* Nees., *Macrolobium* Schreb. sp., *M. macrophyllum* Harms, *Malus pumila* Mill., *Mangifera indica* L., *Mansonia altissima* A. Chev., *Melanorrhoea* Wall. sp., *Melochia umbellata* Stapf., *Microcos coriacea* (Mast.) Burret, *M. pinnatifida* (Mast.) Burret, *Mitragyna stipulosa* O. Ktze. Rev., *Murraya koenigii* Spreng., *Musanga cecropopdes* R. Br., *Myrianthus arboreus* P. Beauv., *Myristica* L. sp., *Myristica dactyloides* Wall., *Napoleana imperialis* P. Beauv., *Nauclea* (*Sarcocephalus*) *diderichii* De Wild., "Nayabu" (Sri Lanka), *Ochthocosmus africanus* Hook., "*Octomeles sumatrana*" (Ohno 1990), *Ongokea gore* Engl., *Pachylobus deliciosus* Pellegr., *Palaquium gutta* Burck., *Pancovia laurentii* De Wild., *Parinari kerstingii* Engl., *Parishia* Hook. f. sp., *Parkia bicolor* A. Chev., *Pithecellobium lobatum* Benth., *Piptadenia africana* Hook, *Piptadeniastrum africanum* Benth., *Protium pittieri* Engl., *Pycnanthus angolensis* (Welw.) Exell., *Quercus* L. sp., *Q. serrata* Roxb., *Randia congolana* De Wild. and Th. Dur., *Ricinodendron heudelotii* (Baill.) Pierre, *Saccharum officinarum* L., *Sagraea laurina* Dalz., *Sandoricum* Cav. sp., *Sapium* P. Browne sp., Sapotaceae sp., *Scorodophloeus zenkeri* Harms, *Shorea* Roxb. ex. C.F. Gaertn. sp., *S. guiso* (Blanco) Blume, *S. macroptera* Dyer, *S. robusta* Gaertn., *Sindora* Miq. sp., *Sorindeia lameirei* De Wild., *Staudtia stipitata* Warb., *Sterculia macrophylla* Vent., *S. oblonga* Mater, *S. villosa* Roxb., *Strombosia glaucesens* Engl., *Strombosiopsis tetrandra* Engl., *Styrax benzoin* Dryand., *Swietenia macrophylla* King., *Synsepalum subcordatum* De Wild., *Tarieta utilis* Sprague, *Tectona grandis* L., *Terminalia ivorensis* A. Chev., *T. superba* Engl., *T. tomentosa* W. and A., *Tessmannia africana* Harms, *T. anomala* Harms, *Tetrapleura* (Thonn.) Taub., *Thalia geniculata* L., *Thea sinensis* L., *Theobroma cacao* L., *Topobea maurofernandeziana* Cogn., *Trichilia heudelotii* Planch., *T. prieureana*

Juss., *Triplochiton scleroxylon* K. Schum., *Turraeanthus africana* Benth., *Vernonia arborea* Ham., *V. conferta* Benth., *Vitis* L. sp., *Vochysia ferruginea* Mart., *Xanthophyllum affine* Korth.

Specimens examined.— (104 ♀; 2 ♂) Type material: Lectotype *Xyleborus declivigranulatus* (♀; NHMW). Holotype *Xyleborus mascarenus* (♀; NHMW). Lectotype *Xyleborus okoumeensis*: In Okumé (♀; NHMW). Paratype *Xyleborus okoumeensis*: W. Africa: Gabun-vinde (♀; NHMW). Allotype *Xyleborus okoumeensis*: Germany: Carlshafen, Hess. Nassau, 17.8.28 (♂; NHMW).

Other material: **Afrotropical Region:** Congo: Yangambi, 1952, C. Donis, z. 1345, Coll. R. Mayne, Com. Ét Bois Congo, R. 2598 (1 ♀; USNM). **Neotropical Region:** United States: Alabama: Baldwin Co., Mobile–Apr 88, C. Kouskelekas (2 ♀; USNM); Quarentine from Florida at Costa Mesa, California, IX.5.2000, Ex. *Dimocarpus longan* (1 ♀; CSCA); Mississippi: Harrison Co., Gulfport, 29 March 1985, John Davis, ex peach (healthy) (1 ♀; USNM); Mississippi: Stone Co. 29 March 1985, G. Weaver, ex plum (healthy) (1 ♀; USNM); Mississippi: Stoneville, Amer. Elm, 6-23-86, J.D. Solomon (2 ♀; USNM). **Oceania:** Hawaiian Islands: Hawaii, Hilo, Hav. Fern Wood, V-16-'53, Working in cut wood, C.J. Davis (1 ♀; USNM); Hawaii, Hilo, X-17-62, ex *Eucalyptus robusta*, R. Nelson (1 ♀; USNM); Oahu, Haleauau Val., 7-54, E.J. Ford Collector (1 ♀; USNM); Oahu: Waianae Mts., 2-55, Ford (3 ♀; CAS); USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21°25′N, 157°51′W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest, A. Newton and M. Thayer, #869, window trap (6 ♀; FMNH). Micronesia: Koror I., Palau Islds., Limestone ridge N. of inlet, 16 Jan. 1948 (1 ♀; USNM). **Oriental Region:** Burma: Burma: Mogaung, X.4.44, Cpt. L.C. Kuitert (1 ♀; USNM). China: China: Suisapa, 1000 m., Lichuan Distr., W. Hupah, VIII.21.48 (1 ♀; CAS); Salango, Kafang, 3.X.1949., F.G. Browne, ex *Ilteoeafus baudii* [?] (1 ♀; USNM). India: India: Dehra Dun. U.P., C.F.C. Beeson, 25.X.1915, ex *Cinnamaum cambhora* (1 ♀; USNM); S. India: Animalia Hills, April 1956, Cichona 3500 ft., P.S. Nathan (2 ♀; USNM); South India: Animalia Hills, Cincohona, V-60, 3500 ft., P.S. Nathan (1 ♀; USNM); S. India: Cinchona, Anamalai Hills, 3500 ft., V.1959, P. S. Nathan (1 ♀; NHMW); S. India: Coffee Re. Sta., 12-29 '59, *Coffea robusta* Lot 60-13752 (1 ♀; USNM); S. India: Madras, Coimbatore, IV-1956 1400 ft., P. S. Nathan (4♀; USNM); South India: Nilgiri Hills, Devala, 3200 ft., X-60, P. S. Nathan (2 ♀; USNM). Indonesia: Java, Leg. Kalshoven (2 ♀; USNM); Java, Bantam, Leg. Kalshoven, Planta nutrix Hena (10 ♀; USNM). Japan: Japan: Matskawa, 27-VII-1980, S.L. Wood (1 ♀; USNM); Okinawa: ID, Nov 16, 1945, F. N. Young (2 ♀; USNM); Japan: Tamagowa, 29-VII-1980, S.L. Wood *Fagus crenatus* (7 ♀; USNM); Japan: Tokyo, Takao, VIII.31.1957, Coll. Akira Nobuchi (2 ♀; USNM). Philippine Islands: Philippines, Mindanao, 1965, Krauss, Cacao trunk (1 ♀, 1 ♂; USNM). Taiwan: Taiwan: Raisya, 24.XI.1934, S. Issiki (1 ♀; NHMW). Formosa, Akau, 1-10.XII.1907, Hans Sauter leg., vend. 23.IV.1908 (♀; NHMW). Thailand: Thailand: Chiengmai Prov., E. Fk. Mae Ping, 56 km N. Chiengmai, 1300', 24-Xi-1964, W.L. and J.G. Peters, at light (1 ♀; CAS). Sri Lanka: Sri Lanka: Col Dist., Labugama, 23 June 1975, S.L. Wood, Collected from branches (10 ♀; USNM); Sri Lanka: Col Dist., Labugama, 23 June 1975, S.L. Wood, Collected from twigs (2 ♀; USNM); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S.L. Wood, Collected from *Liana* (1 ♀; USNM); Sri Lanka: Col Dist., Labugama 23 June 1975, S.L. Wood, Misc. hosts (1 ♀; USNM); Sri Lanka: Gal. Dist., Ugugama, Kanneliya Jungle, 400 ft., 6-12-X-1973, at black light, K.V. Krombein, P. E. Karunarante, P. Fernando, J. Fernando (1 ♀; USNM); Sri Lanka: Kal. Dist., Morapitiya, 250 mtrs., 27 May 1975, S.L. Wood, Misc. hosts (3 ♀; USNM); Sri Lanka: Ceylon: Kan. Dist., Kandy, 1-15 March 1971, Piyadasa and Sompala (1 ♀; USNM); Sri Lanka: Keg. Dis., Kitulgala, 200 m, 30 May 1975, S.L. Wood, Host: Nayabu (1 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 250 m., 27 May 1975, S.L. Wood, Collected from pole (1 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 200 m., 30 May 1975, S.L. Wood, Host: *Doona* sp. (2 ♀; USNM); Sri Lanka: Mat. Dist., Enselwatte, 800 mtrs. 25 May 1975, S.L. Wood, Misc. hosts (7 ♀; USNM); Sri Lanka: Rat, Dist., Gilimale, 17 May 1975, S.L. Wood, Host: *Myristica dactyloides* (3 ♀; USNM); Sri Lanka: Rat. Dist. Gilimale, 17 May 1975, S.L. Wood, Collected from pole (1 ♀; USNM). **Palearctic Region:** Germany: Germany: Carlshafen, Hess. Nassau, 17.8.28 (3 ♀; NHMW).

Xylosandrus curtulus (Eichhoff)

Figure 17.

Xyleborus curtulus Eichhoff, 1869:281. Holotype ♀: Brazil: Patria; IRSNB.
Xylosandrus curtulus (Eichhoff): Wood, 1982:770.

Xyleborus curtuloides Eggers, 1941a:102. Holotype ♀: Guadeloupe (Gourbeyre); Eggers Collection (not listed by Anderson and Anderson, 1971 or Schedl, 1979a). Synonymy: Wood, 1982:770.

Xyleborus biseriatus Schedl, 1963b:226. Holotype ♀: Nova Teutonia, Santa Catarina, Brazil; NHMW. Synonymy: Wood, 1973:187.

Xylosandrus strumosus Schedl, 1972:73. Holotype ♀: Brasilien, Corcovado, Guanabara; NHMW. Synonymy: Wood and Bright, 1992:793.

Anisandrus zimmermanni Hopkins, 1915:67. Holotype ♀: Biscayne, Florida; USNM. Synonymy: Wood, 2007: 467.

Xylosandrus zimmermanni (Hopkins): Wood, 1962:79.

NOTES.— Wood and Bright (1992) first list *Xylosandrus strumosus* as a synonym of *Xylosandrus curtulus*. The synonymy is referenced as "Wood 1992: (in press)", but the synonymy did not appear in another publication.

DIAGNOSIS.— Female 1.3–1.5 mm long; 2.1 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibiae with 7 socketed teeth. Elytra 1.3 times longer than wide; 1.5 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. compactus* (Fig. 14) and *X. pusillus* (Fig. 36). *Xylosandrus curtulus* can be distinguished from these species by the following characters: pronotal disc glabrous, except for a dense patch of short, erect, hair-like setae basally, indicating the presence of a pronotal-mesonotal mycangium; and elytra strongly arched from base to middle of declivity.

DISTRIBUTION.— **Nearctic Region (Introduced):** United States (Florida). **Neotropical Region:** Antilles Islands (Guadeloupe), Brazil, Colombia, Costa Rica, Guatemala, Honduras, Mexico (Chiapas, Colima, Hidalgo, Nayarit, Oaxaca, San Luis Potosi, Varacruz), Venezuela.

HOSTS.— *Acer rubrum* L., "*Anonillo*" (Guatemala), *Ardisia* Gaertn. sp., *Byrsonima cotinifolia* H. B. and K., *Calliandra confusa* Sparque and Riley, *Cedrela odorata* L., *Chrysobalanus* L. sp., *Coffea canephora* var. *robusta* (Linden) A. Chev., *Cupania guatemalensis* Radlk., *Dodonaea viscose* Jacq., *Ficus* L. spp., *Inga* Scop. sp., *Nectandra* Roll. ex Rottb. sp., *Ocotea catesbyana* Sarq., *Phoradendron robustissimum* Eichler, *Phoradendron* Nutt. spp., *Rheedia edulis* Planch. and Triana., *Serjania* Mill. sp., *Spondias mombin* L., *Tabebuia* Gomes ex. DC. sp.

SPECIMENS EXAMINED.— (86 ♀; 3 ♂) TYPE MATERIAL: Holotype *Xyleborus biseriatus*; (♀; NHMW). Holotype *Xylosandrus strumosus* (♀; NHMW). Holotype *Anisandrus zimmermanni* (♀; USNM).

OTHER MATERIAL: **Nearctic Region:** United States: Florida: Sebring, 6-20-1951, Price Beamers–Wood (1 ♀; USNM); Florida: Sebring, 6-20-1951, Price Beamers–Wood, *Ardisia* (7 ♀, 1 ♂: USNM); Florida: Sebring, 6-20-1951, Price Beamers–Wood, *Ocotea catsibiana* (1 ♀USNM); Florida: Sebring, 6-20-1951, Price Beamers–Wood, Red Maple (2 ♀, 1 ♂; USNM). **Neotropical Region:** Colombia: Colombia: Caicedonia near Sevilla, Aug. 1959, Coffee branches, Leg. Duque (1 ♀; USNM); Colombia: El Bosque, Caicedonia

(V.), Junio 1959, J. Restrepo, en Café (11 ♀, 1 ♂; USNM); Colombia: 1959, leg. Beteem (1 ♀; USNM). Costa Rica: Costa Rica: Guapiles, Lim. 300 ft., VIII-22-'66, S. L. Wood, unknown vine (2 ♀; USNM); Costa Rica: Santa Ana, S.J., 4000 ft., VII-1-1963, S.L. Wood, Coffee (1 ♀; USNM); Costa Rica: Santa Ana, S.J., 4000 ft., VIII-30-1963, S.L. Wood, *Rheedia edulis* (1 ♀; USNM); Costa Rica: Santa Ana, S.J., 4000 ft., VIII-30-1963, S.L. Wood, unknown sapling (3 ♀; USNM); Costa Rica: Santa Ana, S.J., 400 ft., VIII-1-1963, S.L. Wood, *Cupania guatemalensis* (9 ♀; USNM); Costa Rica: San Ignacio, S.J., 4700 ft., VIII-5-1963, S. L. Wood, unknown sapling (1 ♀; USNM); Costa Rica: Pandora, Lim., 150 ft., VIII-23-1963, S. L. Wood, unknown shrub (4 ♀; USNM); Costa Rica: Tapnti Cart., 400 ft., VIII-17-1963, S.L. Wood, *Calliandra confusa* (1 ♀; USNM). Guatemala: Guatemala: Palin, Esquintla, 100 ft., V-19-1964, S.L. Wood, *Anonillo* (1 ♀; USNM); Guatemala: Rodeo Esquintla, 500 ft., VI-4-1964, S. L. Wood, Unknown vine (1 ♀; USNM); Guatemala: Volcan de Agua, 3000 ft., V-19-1964, S.L. Wood, unknown twigs (1 ♀; USNM); Guatemala: Volcan de Agua, 3000 ft., V-19-1964, S.L. Wood, unknown broken branch (1 ♀; USNM). Honduras: Honduras: Zamorano, Moraz, 2200 ft., IV-18-1964, S.L. Wood, *Phoradendron robustissimum* (1 ♀USNM); Honduras: Zamorano, Moraz, 2200 ft., Serjania (1 ♀; USNM). Mexico: Mexico: 2 mi W Armeria, Col., VI-28-1965, 200 ft., S.L. Wood, *Phoradendron* (2 ♀; USNM); Mexico: El Salto, S.L.P., VI-19-53, taken on *Ficus* (1 ♀; USNM); Mexico: Morelos, Ruinas de Xochicalco, S-322, 22E 82, 1200 ms n m, Col Atkinson and Equihua, Hosp. *Dodonaea viscosa* (1 ♀; USNM); Mexico: Laguna Sta. Maria N., VII-6-1965, 3000 ft., S.L. Wood, unknown vine (1 ♀; USNM); Mexico: Romero 12 mi S, VI-24-1967, OAX, S.L. Wood, *Phoradendron* (1 ♀; USNM); Mexico: 5 mi N Rosamorada N., VII-15-1965, 300 ft., S.L. Wood, unknown broken branch (2 ♀; USNM); Mexico: Romeo, 23 mi N VC, 300 ft., S.L. Wood, unknown branch (1 ♀; USNM); Mexico: Tapachula Chis, 21 VIII 82, Col. A. B. Celis, *Coffea conephora* var. *robusta* (1 ♀; USNM); Mexico: Vera Cruz, 16 mi S Tecolutla, VI-26.53 (8♀; USNM). Venezuela: Venezuela: S. of Barrancas, Barinas, 150 m., XI-5-69, S.L. Wood, *Spondias mombin* (1 ♀; USNM); Venezuela: 9 km S. of Barrancas, Barinas, 150 m., XI-15-69, S.L. Wood, *Inga* (1 ♀; USNM); Venezuela 40 km, E. Canton-Barinas, III-8-1970, 70 m., S. L. Wood, unknown vine (1 ♀; USNM); Venezuela: 20 km SW El Vigia, Merida, XII-10 69, el. 50 m., S.L. Wood (1 ♀; USNM); Venezuela: Rancho Grande, Aragua, 1100 m., IV-9-1970, S.L. Wood, *Tabebuia* (3 ♀; USNM); Venezuela: Rancho Grande, Aragua, 1100 m., IV-9-1970, S.L. Wood, *Nectandra* sp. (5 ♀; USNM); Venezuela: 40 km SE Socopo, Barinas, I-25-1970, 150 m., S.L. Wood, Bejuco Blanco (1 ♀; USNM).

***Xylosandrus derupteterminatus* (Schedl)**
Figure 18.

Xyleborus derupteterminatus Schedl, 1951:64. Holotype ♀: Java, Mount Gede IX.1932L. G.E. Kalshoven Coll., NHMW.
Xylosandrus derupteterminatus (Schedl): Schedl, 1964:213.

Diagnosis.— Female 2.0–2.3 mm long; 2.0 times longer than wide. Body dark brown to black; antennae and legs same color as body. Frons punctate, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with dense patch of short, erect setae indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 13 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep, abruptly separated from disc. Declivity flattened, lateral margin carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. morigerus* (Fig. 35) and X. *terminatus* (Fig. 43). *Xylosandrus derupteterminatus* can be distinguished from *X. morigerus* by the following characters: face of elytral declivity flattened; and 5 striae visible on declivity. *Xylosandrus derupteterminatus* can be distinguished from *X. terminatus* by the following characters: larger species, 2.0–2.3 mm long; interstrial setae shorter than the width of second declivital interstriae; and declivital interstriae uniseriate granulate.

Distribution.— **Oriental Region:** Indonesia (Java, Moluccas, Sulawesi).

Hosts.— Unknown.

Specimens examined.— (10 ♀; 0 ♂) Type material: Holotype *Xyleborus derupteterminatus* (♀;NHMW).

Other material: **Oriental Region:** Indonesia: Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot A, ca 200 m Lowland forest, May-85, Flight intercept trap (4 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot A, ca 200 m Lowland forest, Dec. 1985, suspended carrion (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Apr-85, Flight intercept trap (2 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Feb-85, Flight intercept trap (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., G.Mogogonipa summit, 1008 m., 22-24.x.85, yellow plate (1 ♀; RAB).

Xylosandrus deruptulus (Schedl)

Figure 19.

Xyleborus deruptulus Schedl, 1942b:37. Lectotype ♀: Java, Mount Dede, 800 m, VIII-1923, Nr 54, Kalshoven; NHMW; designated by Schedl, 1979a:78.
Xylosandrus deruptulus (Schedl): Schedl, 1964:213.

Diagnosis.— Female 1.8 mm long; 2.2 times longer than wide. Body brown; antennae and legs light brown. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of appressed, hair-like setae; setae less dense on disc. Specimen examined too damaged to determine whether pronotal mycangial setae are present. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate. Interstriae granulate, uniseriate. Specimen examined too damaged to determine states of declivital setae and setae not mentioned in original description (Schedl 1942b).

This species is morphologically similar to *X. assequens* (Fig. 10). *Xylosandrus deruptulus* can be distinguished from *X. assequens* by the following characters: more elongate, 2.2 times longer than wide; elytral disc with interstriae more sparsely punctured, multiseriate only on first interstriae; declivital interstriae uniseriate granulate; and declivital surface shining, not matte.

Distribution.— **Oriental Region:** Indonesia (Java).

Hosts.— Unknown.

Specimens examined.— (1 ♀; 0 ♂) Type material: Lectotype *Xyleborus deruptulus* (♀; NHMW).

Xylosandrus discolor (Blandford)

Figure 20.

Xyleborus discolor Blandford, 1898:429. Holotype ♀: Ceylon, E.E. Green; BMNH.
Xylosandrus discolor (Blandford): Browne, 1963:55.
Xyleborus posticestriatus Eggers, 1939b:119. Lectotype ♀: Formosa (Taihoku); USNM; designated by Anderson and Anderson, 1971:26. Synonymy: Schedl, 1958:149.
Xylosandrus posticestriatus (Eggers): Nunberg, 1959:434.

Notes.— Wood and Bright (1992) list *Xylosandrus posticestriatus* Eggers as a separate species. However, we agreed with Schedl (1958) and consider it a synonym of *X. discolor*.

Diagnosis.— Female 1.8–2.0 mm long; 1.8 times longer than wide. Body bicolored; pronotum distinctly lighter than elytra; pronotum light brown and elytra dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of erect, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-punctate, with sculpture separated by distance less than or equal to their size. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4–5 socketed teeth on lateral margin; meso- and metatibiae with 8–9 socketed teeth. Elytra of equal length and width; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 9), *X. discolor*, *X. ferinus* (Fig. 23), and *X. mesuae* (Fig. 30). *Xylosandrus discolor* can be distinguished from these species by the following characters: elytral declivity steep and abruptly separated from disc, and declivital striae and interstriae with a dense vestiture of appressed setae.

Distribution.— **Australian Region:** Australia (Queensland). **Oceania:** Micronesia. **Oriental Region:** Burma, China (Fujian, Guangdong, Sichuan, Yunnan), India (Andaman Islands, Assam, Tamil Nadu, Uttar Pradesh), Indonesia (Java), Malaysia, Sri Lanka, Taiwan, Thailand.

Hosts.— *Ailanthus altissima* (Mill.) Swingle, *Albizia* Benth. sp., "Avocado" (Java), *Bauhinia variegata* L., *Camellia sinensis* Kuntze, *Cassia multijuga* Rich., *Castanopsis fargesii* Franch., *Cedrela toona* Roxb. ex Rottler and Willd., *Chloroxylon swietenia* DC., *Coffea* L. spp., *Coffea arabica* L., *C. robusta* L. Linden, *Cinnamomum camphora* (L.) J. Presl., *Eupatorium* L. sp., *Grevillea robusta* A. Cunn., *Hevea brasiliensis* (Willd. ex A. Juss) Műll. Arq., "*Igall* sp." (Thailand), *Juglans nigra* L., "Liana" [woody vine] (Sri Lanka) sp., *Machilus indica* Kurz., "Mango" (Thailand), *Pterospermum acerifolium* Willd., "Rukaththana" (Sri Lanka), *Rhus chinensis* Mill., *Sophora japonica* L., *Swietenia mahagoni* (L.) Jacq., *Tephrosia candida* DC., *Terminalia myriocarpa* Van Heurck and Műll. Arq., *T. procera* Roxb., *Theobroma cacao* L., *Vitis vinifera* L.

Specimens examined.— (61 ♀; 4 ♂) Type material: Lectotype *Xyleborus posticestriatus*: Formosa: Taihoku, 10.VII.1934, Col. M. Chujo (♀; NHMW). Paralectotype *Xyleborus posticestriatus*: XI.1926 (locality unreadable) (♂; NHMW).

Other material: **Australian Region:** Australia (Queensland): Australia: N. QLD, Iron Range, 26-31.X.1991, Wood, Dunn, and Hasenpusch (3 ♀; RAB); NE.Q: 16°54′S x 145°42′E, Whitefield Range, 550 m,

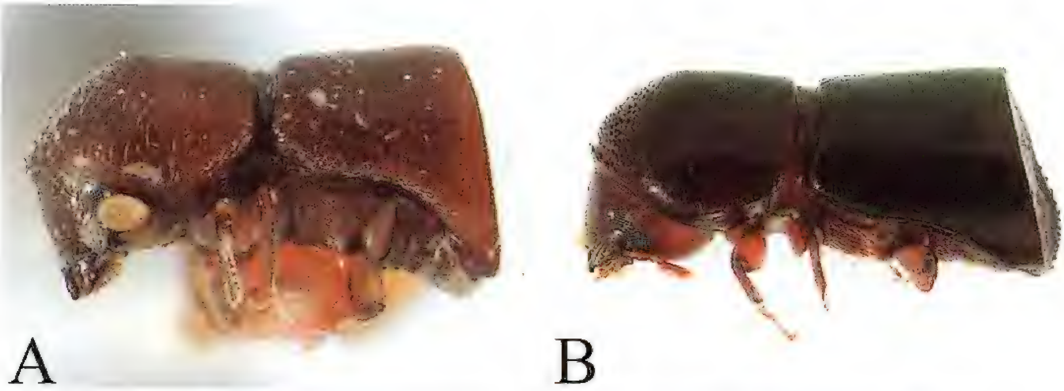


FIGURE 3. Lateral habitus of *Amasa cylindrotomicus* n. comb., female (A) and *Amasa bicostatus*, female (B).

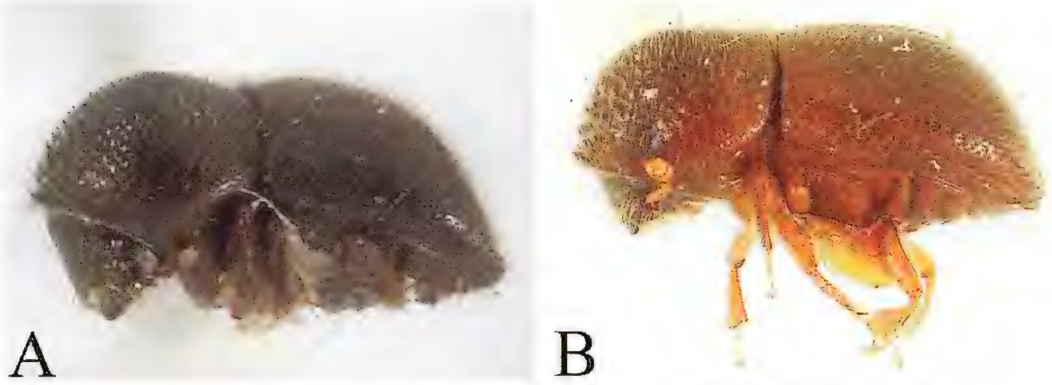


FIGURE 4. Lateral habitus of *Anisandrus ursulus* n. comb., female (A) and *Anisandrus sayi*, female (B).

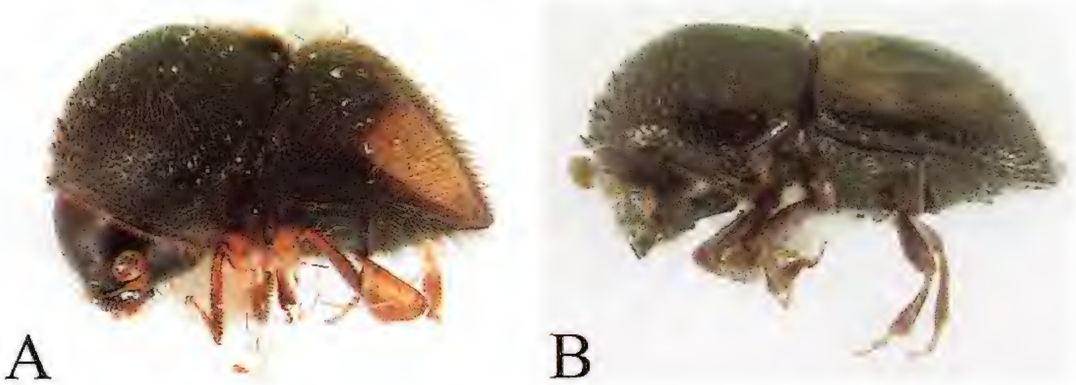


FIGURE 5. Lateral habitus of *Cnestus improcerus* n. comb., female (A) and *Cnestus pseudosuturalis*, female (B).

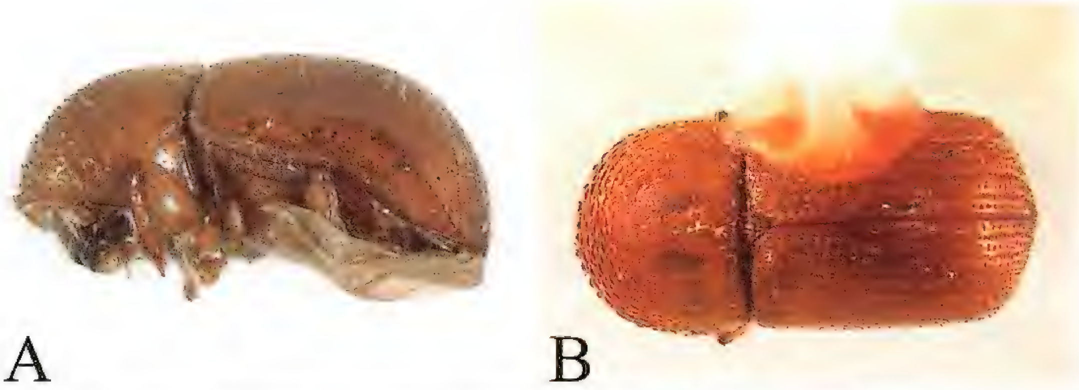


FIGURE 6. Lateral (A) and dorsal (B) views of *Xylosandrus abruptulus*, 1.9–2.1 mm, female lectotype.

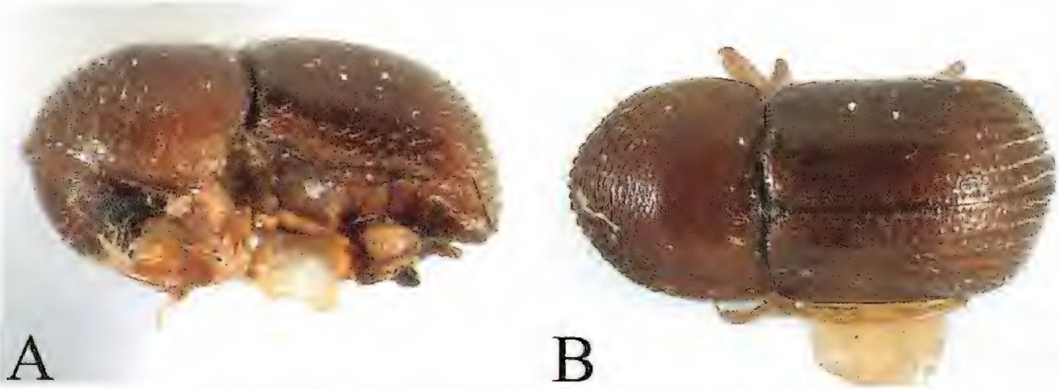


FIGURE 7. Lateral (A) and dorsal (B) views of *Xylosandrus adherescens*, 2.0 mm, female holotype.

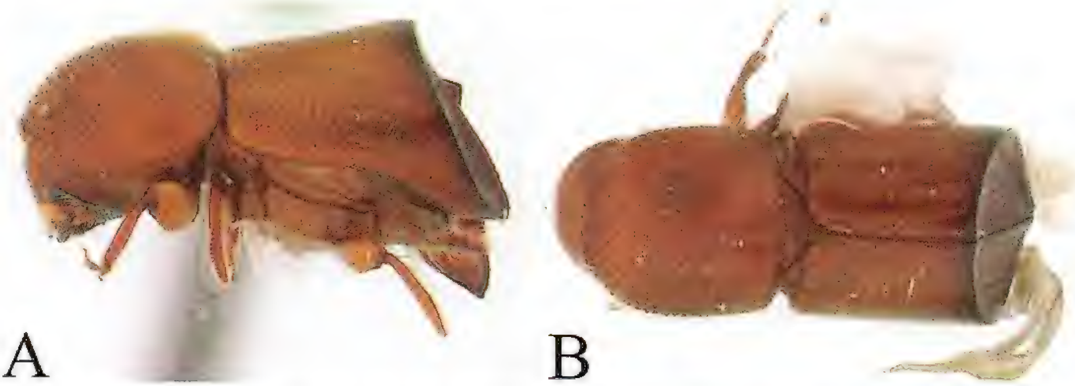


FIGURE 8. Lateral (A) and dorsal (B) views of *Xylosandrus amputatus* n. comb., 2.7–2.9 mm, female.

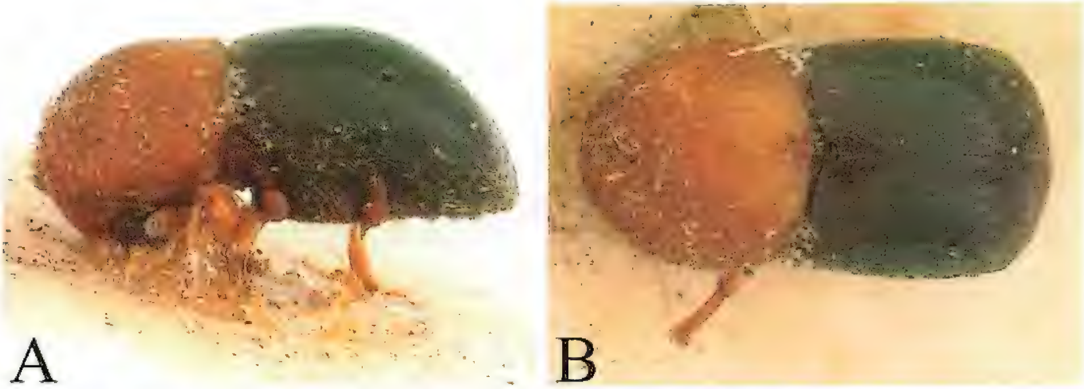


FIGURE 9. Lateral (A) and dorsal (B) views of *Xylosandrus arquatus*, 2.3–2.5 mm, female.

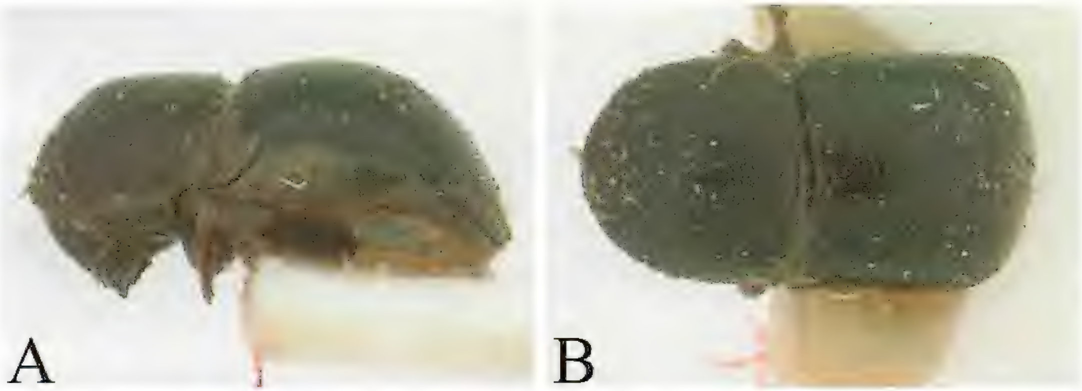


FIGURE 10. Lateral (A) and dorsal (B) views of *Xylosandrus assequens*, 1.6–2.3 mm, female, holotype.

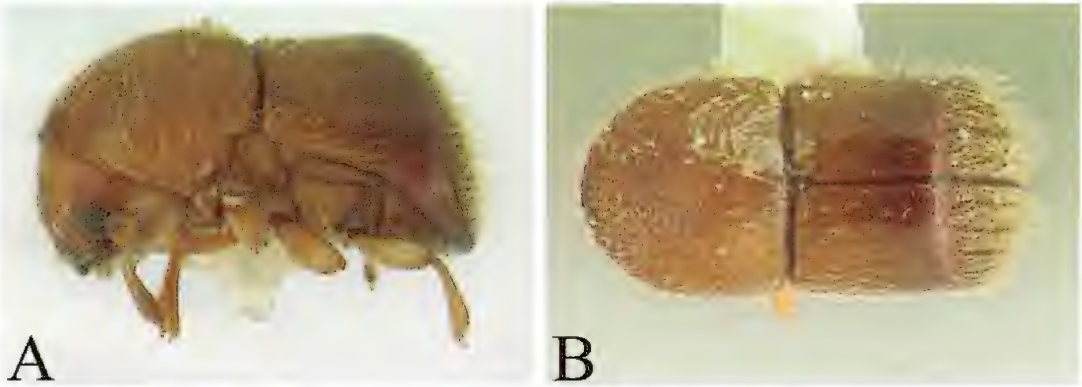


FIGURE 11. Lateral (A) and dorsal (B) views of *Xylosandrus borealis*, 2.0–2.1 mm, female.

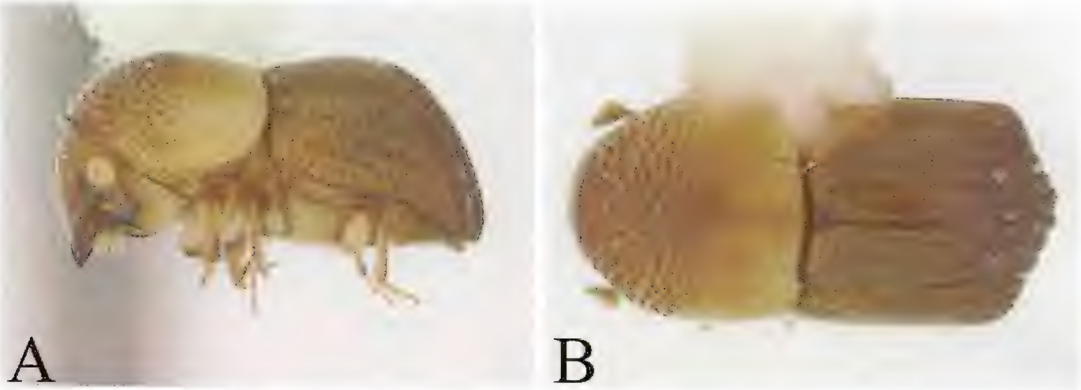


FIGURE 12. Lateral (A) and dorsal (B) views of *Xylosandrus borneensis* n. sp., 1.5–1.6 mm, female holotype.

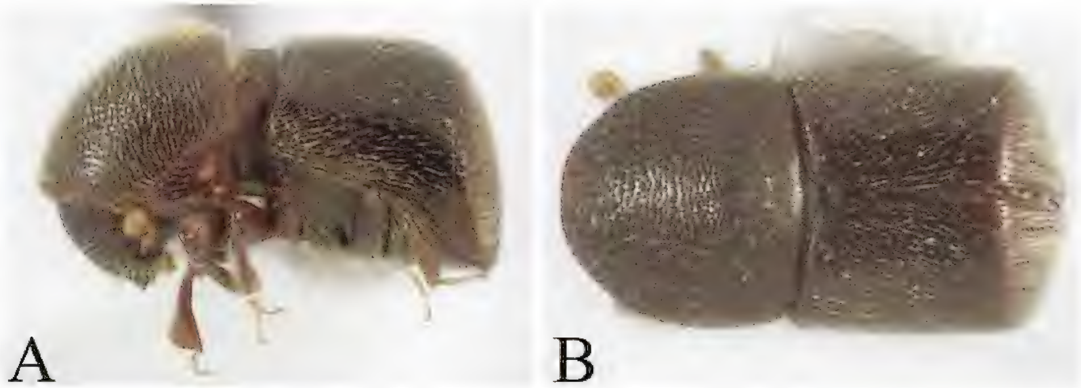


FIGURE 13. Lateral (A) and dorsal (B) views of *Xylosandrus brevis*, 2.5–2.8 mm, female.

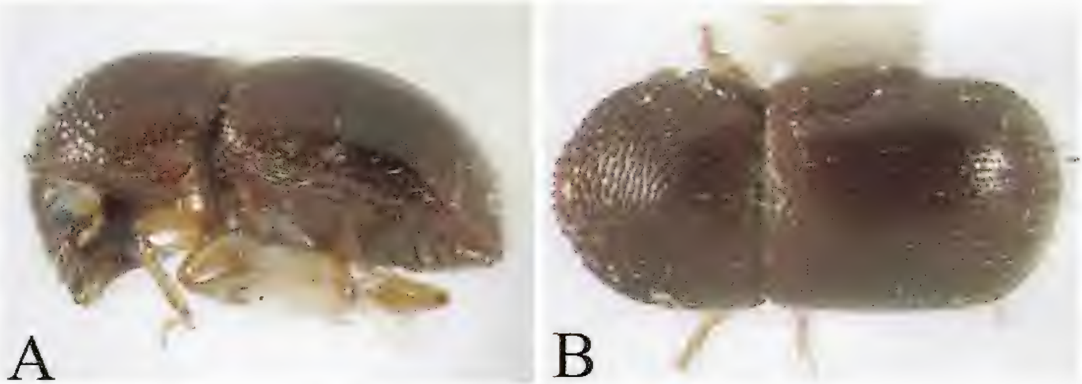


FIGURE 14. Lateral (A) and dorsal (B) views of *Xylosandrus compactus*, 1.4–1.9 mm, female.

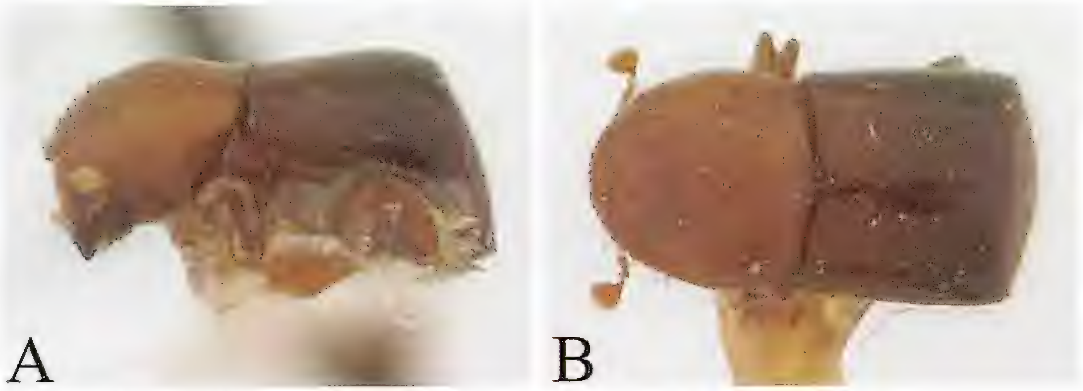


FIGURE 15. Lateral (A) and dorsal (B) views of *Xylosandrus corthyloides*, 2.7–3.0 mm, female lectotype.

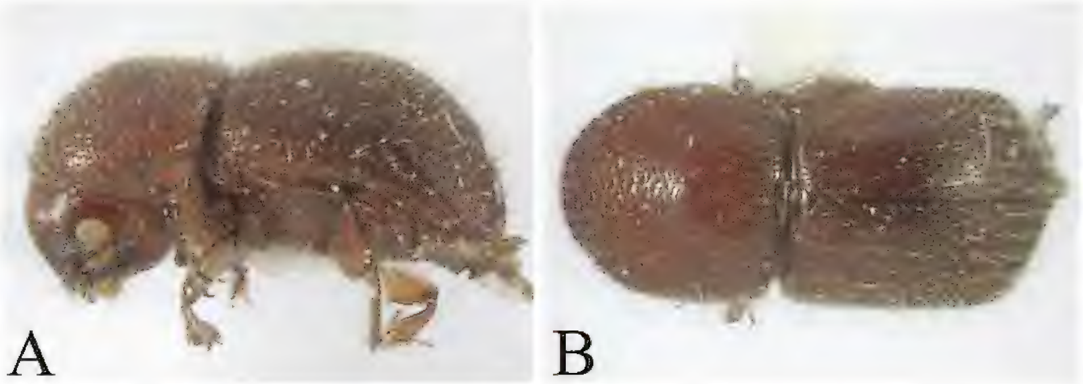


FIGURE 16. Lateral (A) and dorsal (B) views of *Xylosandrus crassiusculus*, 1.7–2.9 mm, female

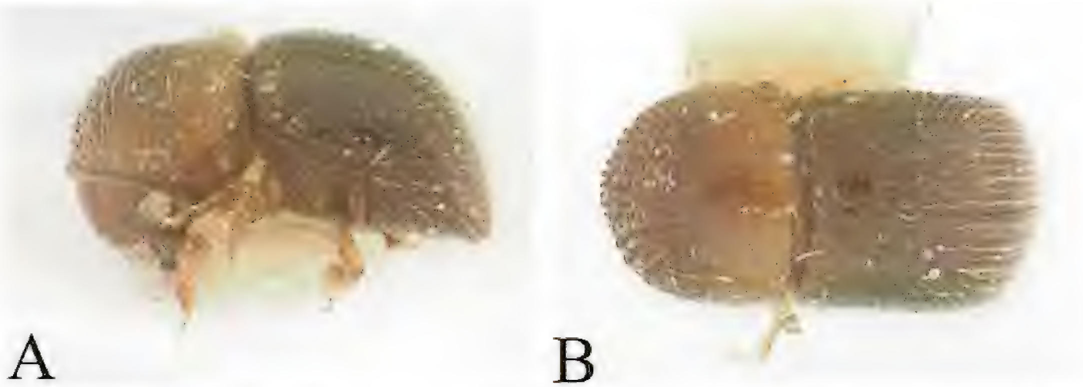


FIGURE 17. Lateral (A) and dorsal (B) views of *Xylosandrus curtulus*, 1.3–1.5 mm, female holotype of synonym *X. biseriatus*.

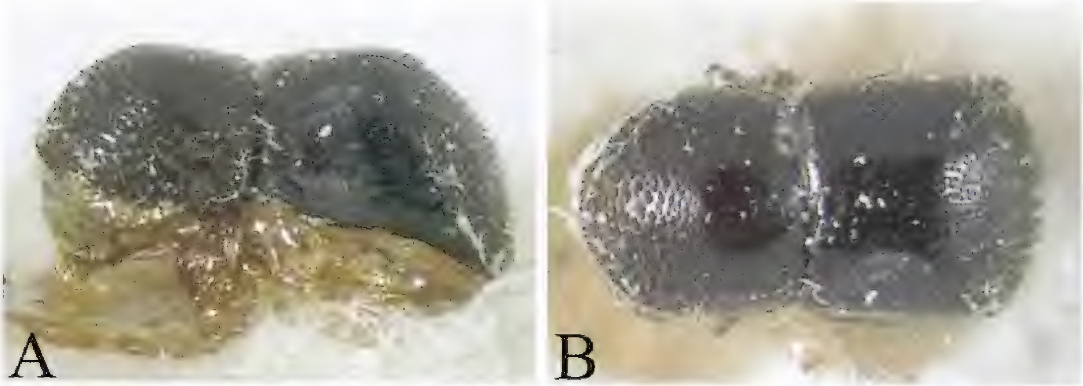


FIGURE 18. Lateral (A) and dorsal (B) views of *Xylosandrus derupteterminatus*, 2.0–2.3 mm, female holotype.

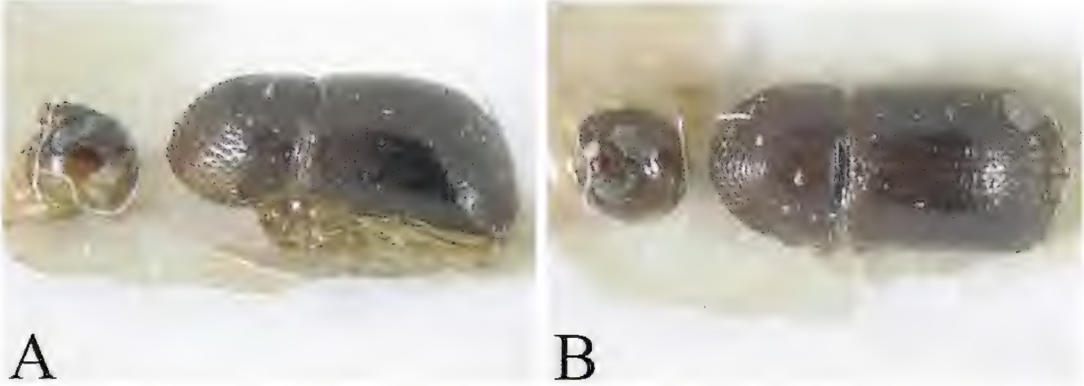


FIGURE 19. Lateral (A) and dorsal (B) views of *Xylosandrus deruptulus*, 1.8 mm, female lectotype.

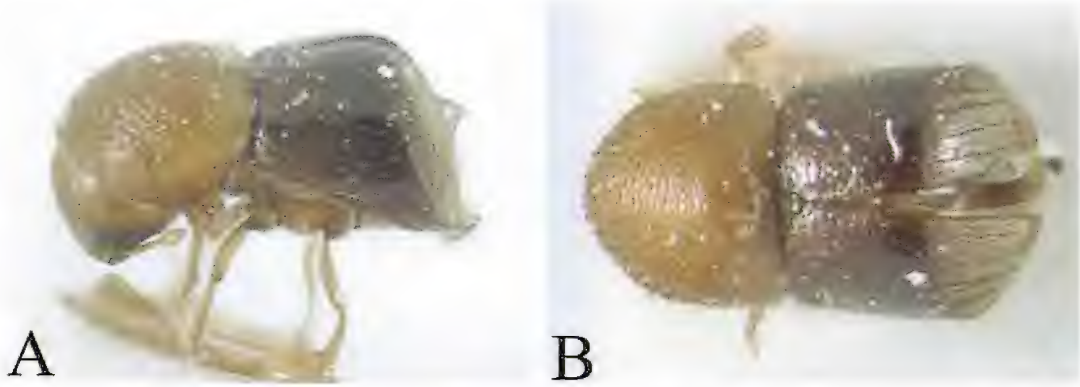


FIGURE 20. Lateral (A) and dorsal (B) views of *Xylosandrus discolor*, 1.8–2.0 mm, female.

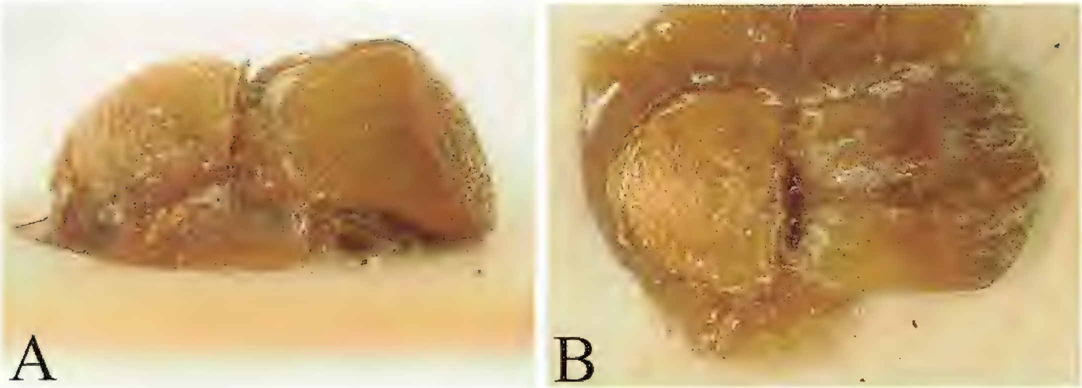


FIGURE 21. Lateral (A) and dorsal (B) views of *Xylosandrus diversepilosus*, 1.8–2.3 mm, female holotype.

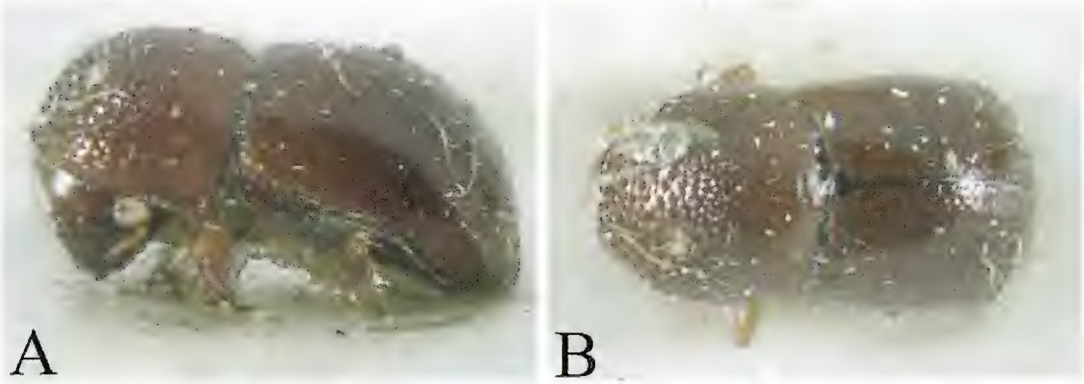


FIGURE 22. Lateral (A) and dorsal (B) views of *Xylosandrus eupatorii*, 1.8–2.1 mm, female cotype.

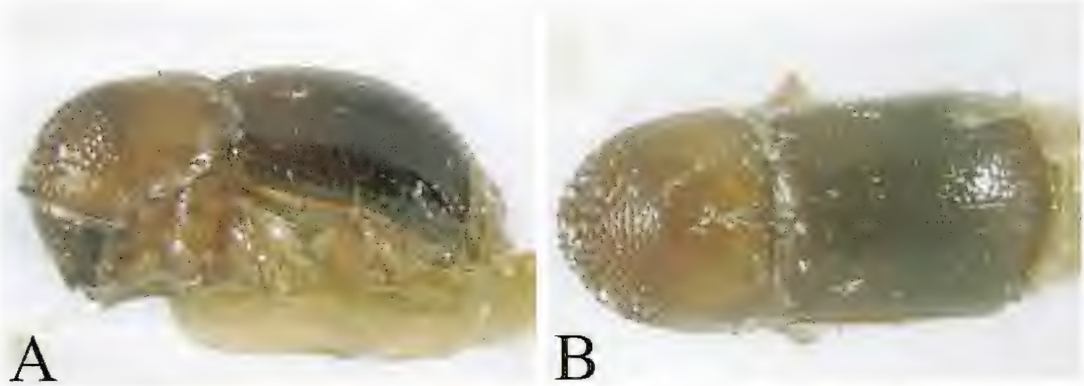


FIGURE 23. Lateral (A) and dorsal (B) views of *Xylosandrus ferinus*, 1.6–1.8 mm, female lectotype.

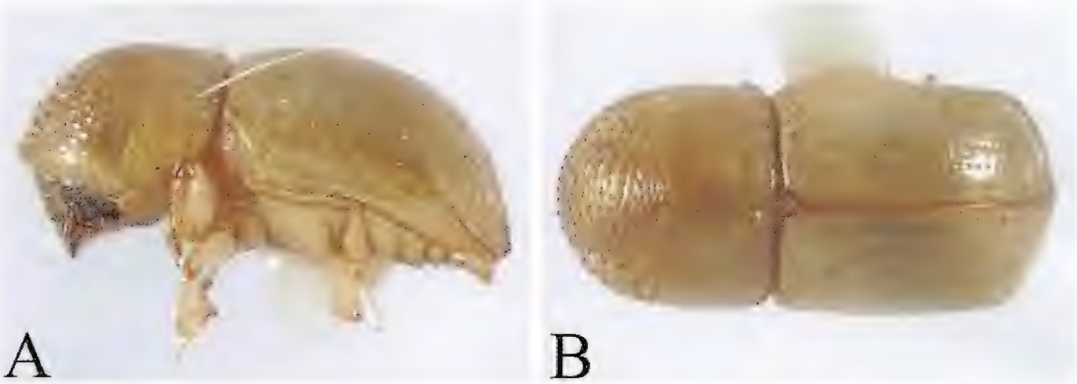


FIGURE 24. Lateral (A) and dorsal (B) views of *Xylosandrus germanus*, 1.9–2.5 mm, female.

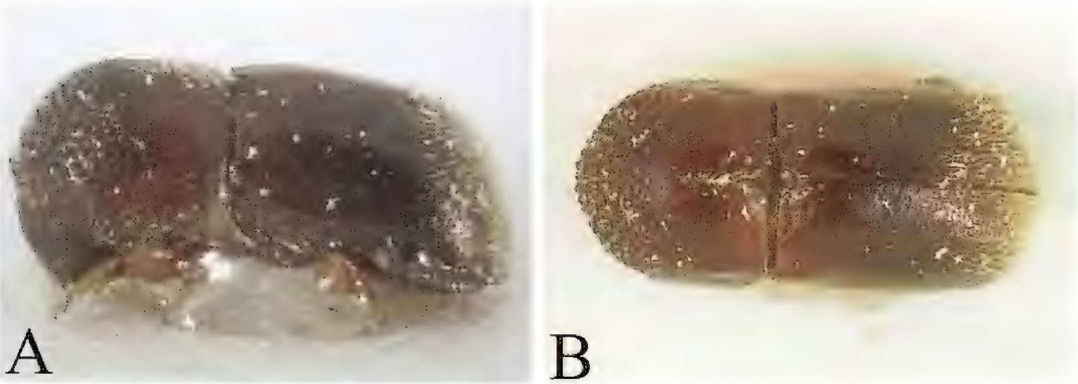


FIGURE 25. Lateral (A) and dorsal (B) views of *Xylosandrus hirsutipennis*, 1.9–2.2 mm, female paratype.

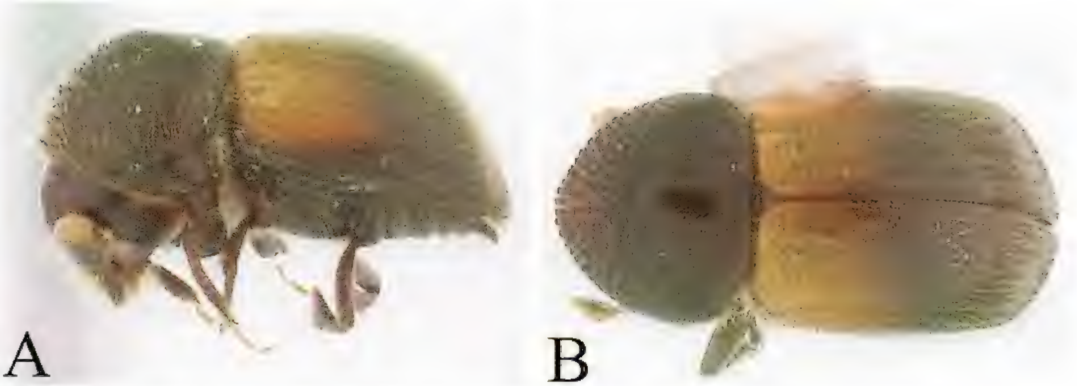


FIGURE 26. Lateral (A) and dorsal (B) views of *Xylosandrus hulcri* n. sp., 2.4–2.7mm, female holotype.

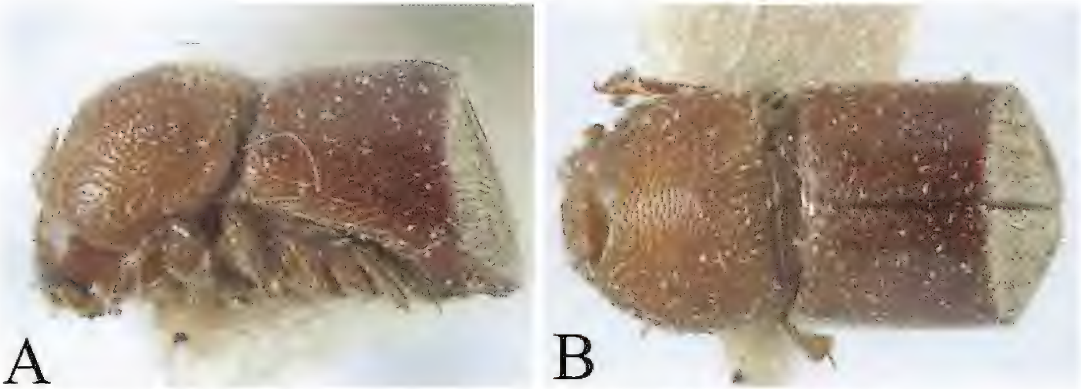


FIGURE 27. Lateral (A) and dorsal (B) views of *Xylosandrus jaintianus*, 3.0 mm, female holotype.

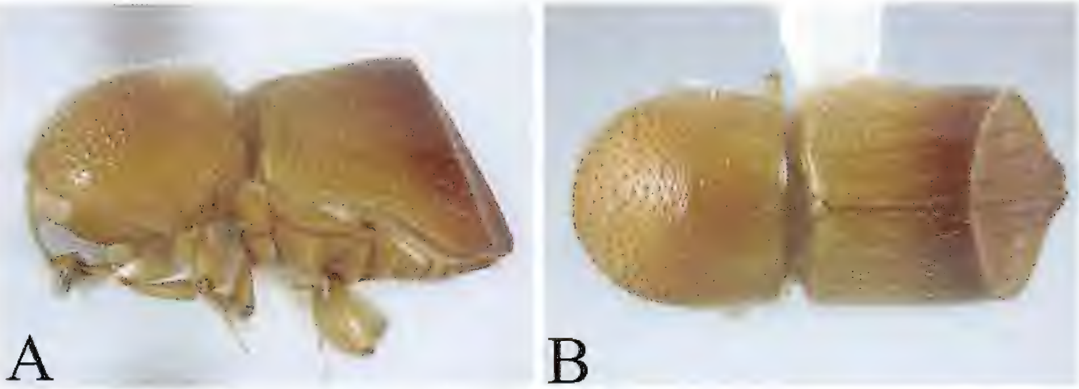


FIGURE 28. Lateral (A) and dorsal (B) views of *Xylosandrus mancus*, 2.9–3.3 mm, female.

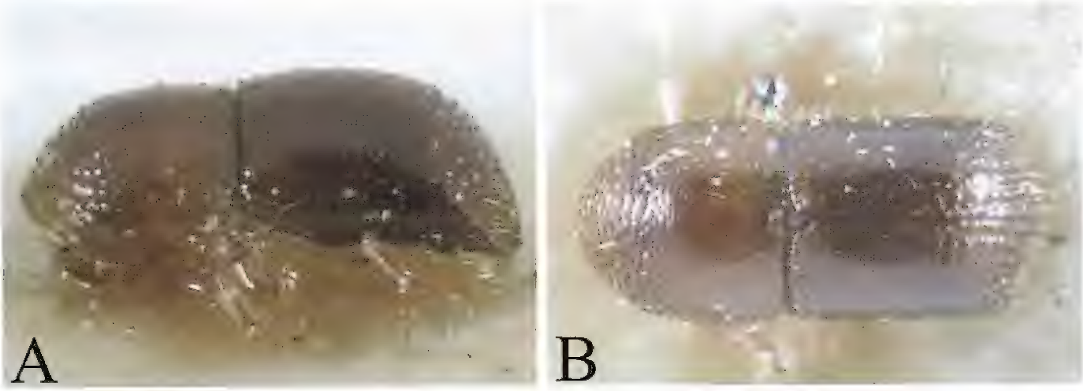


FIGURE 29. Lateral (A) and dorsal (B) views of *Xylosandrus mediocris*, 1.4 mm, female.

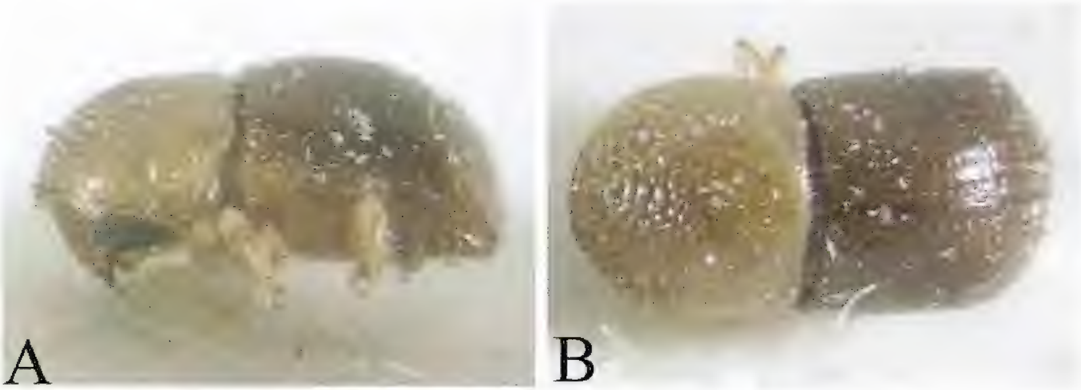


FIGURE 30. Lateral (A) and dorsal (B) views of *Xylosandrus mesuae*, 1.1–1.3 mm, female.

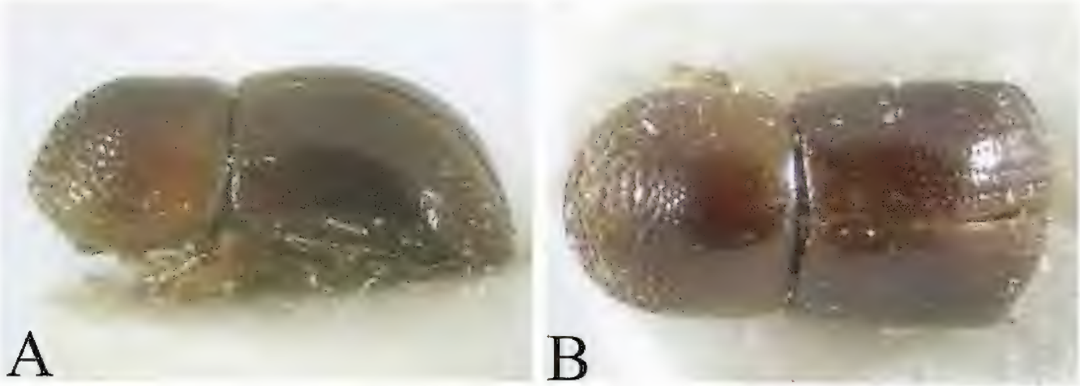


FIGURE 31. Lateral (A) and dorsal (B) views of *Xylosandrus metagermanus*, 1.8 mm, female holotype.

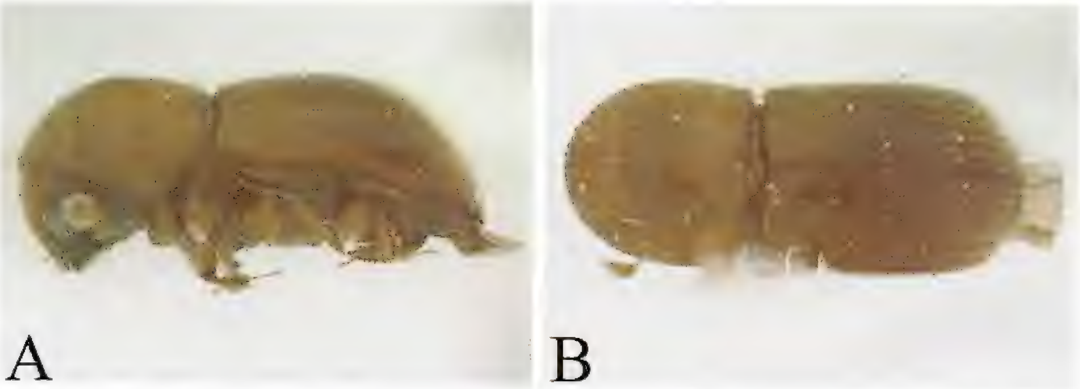


FIGURE 32. Lateral (A) and dorsal (B) views of *Xylosandrus mixtus* n. comb., 2.6–2.7 mm, female holotype.

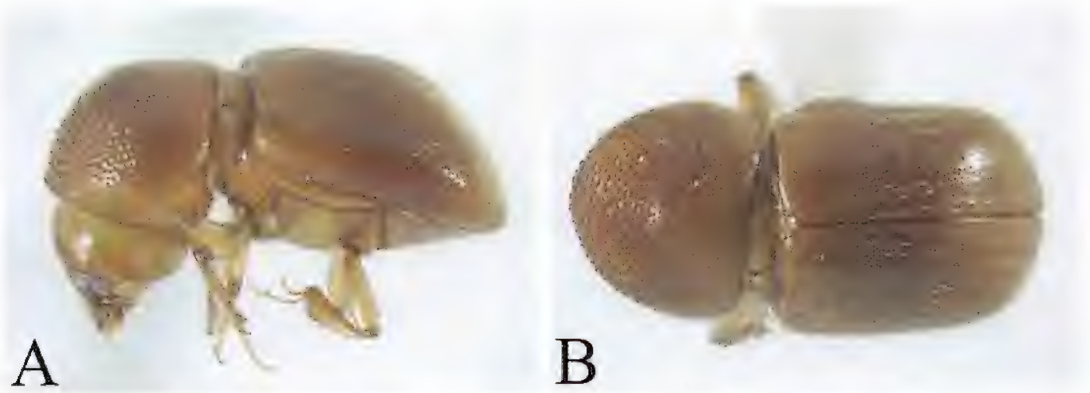


FIGURE 33. Lateral (A) and dorsal (B) views of *Xylosandrus monteithi*, 3.0–3.4 mm, female paratype.

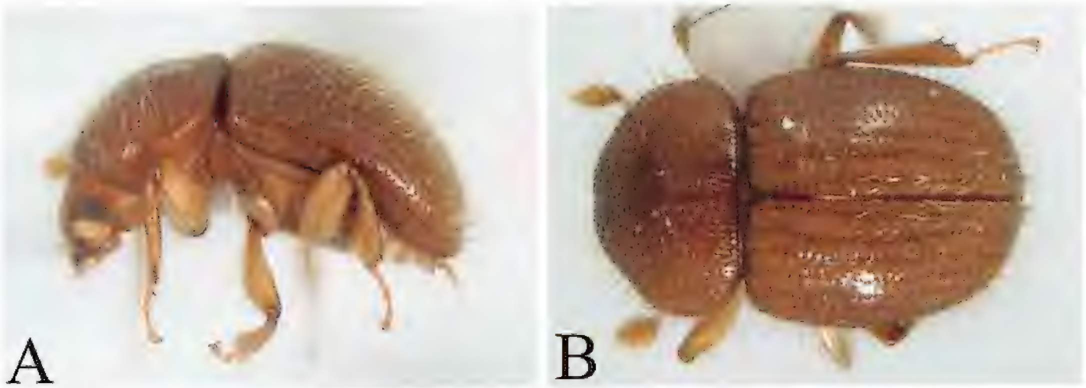


FIGURE 34. Lateral (C) and dorsal (D) views of *Xylosandrus monteithi*, 2.5 mm, male allotype.

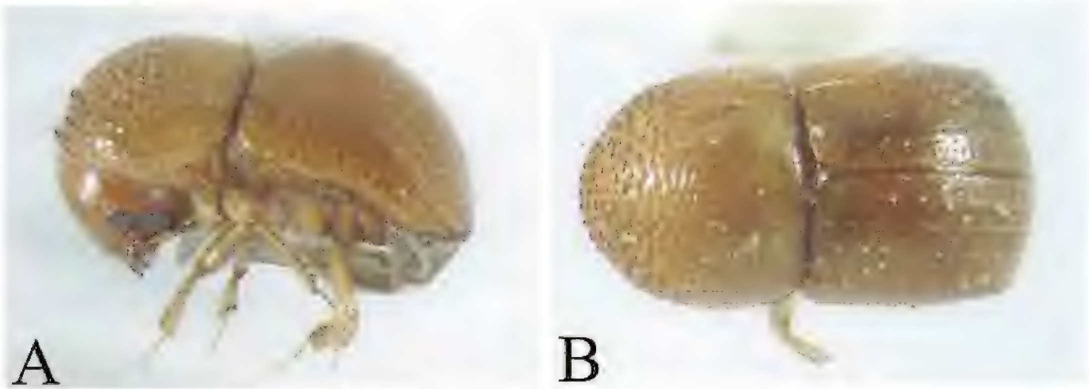


FIGURE 35. Lateral (A) and dorsal (B) views of *Xylosandrus morigerus*, 1.5–2.0 mm, female.

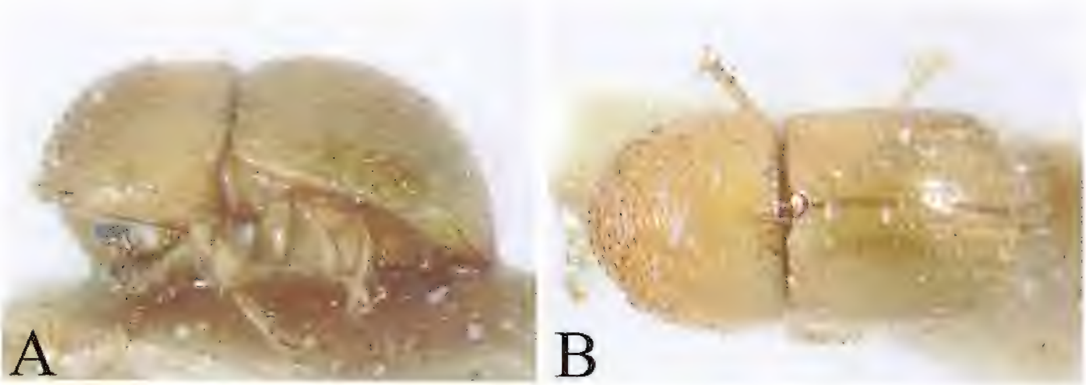


FIGURE 36. Lateral (A) and dorsal (B) views of *Xylosandrus pusillus*, 1.5–1.7 mm, female holotype.

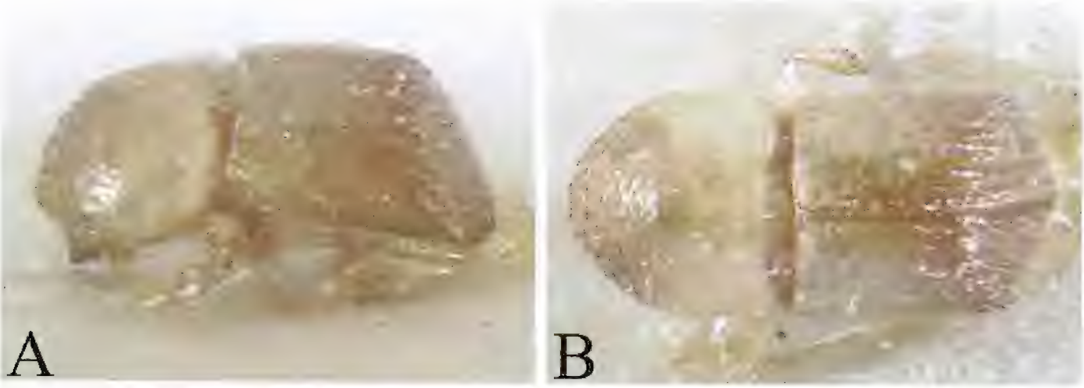


FIGURE 37. Lateral (A) and dorsal (B) views of *Xylosandrus pygmaeus*, 1.3–1.4 mm, female holotype.

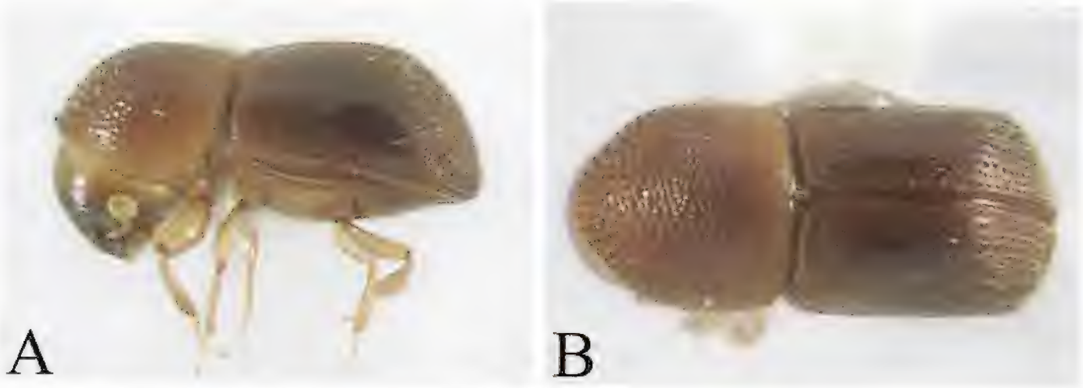


FIGURE 38. Lateral (A) and dorsal (B) views of *Xylosandrus queenslandi*, 1.6–1.9 mm, female paratype.

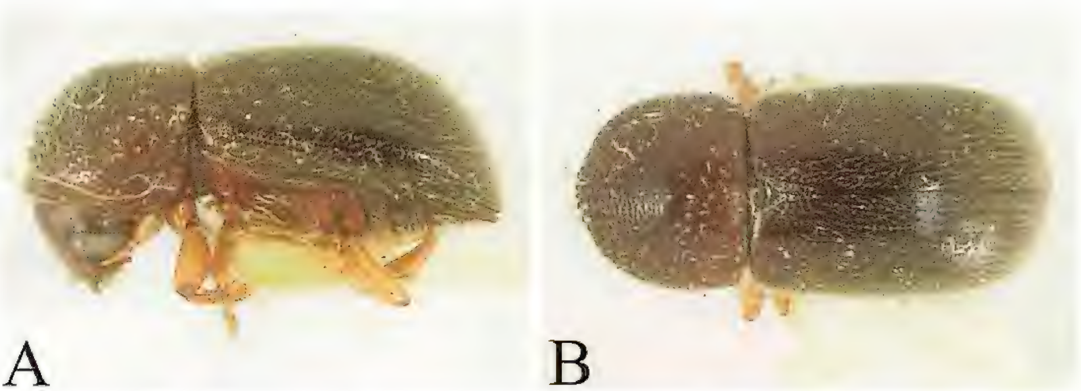


FIGURE 39. Lateral (A) and dorsal (B) views of *Xylosandrus rotundicollis* n. comb., 2.5 mm, female holotype.

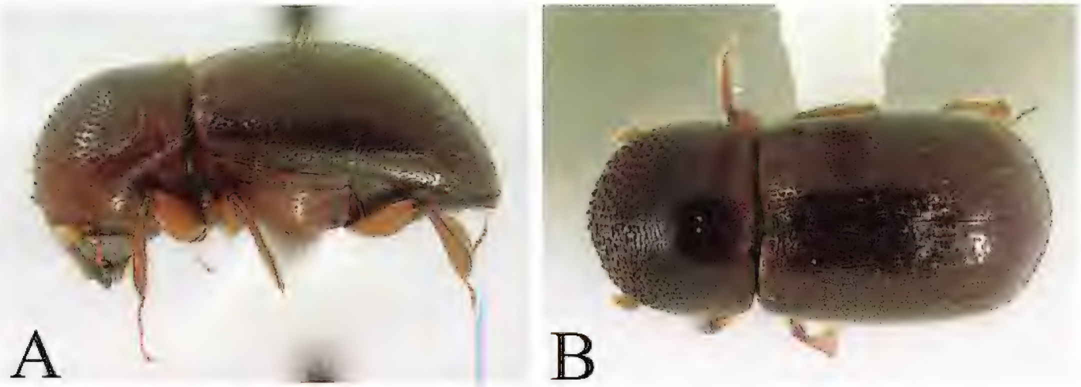


FIGURE 40. Lateral (A) and dorsal (B) views of *Xylosandrus russulus* n. comb., 3.4–4.2 mm, female.

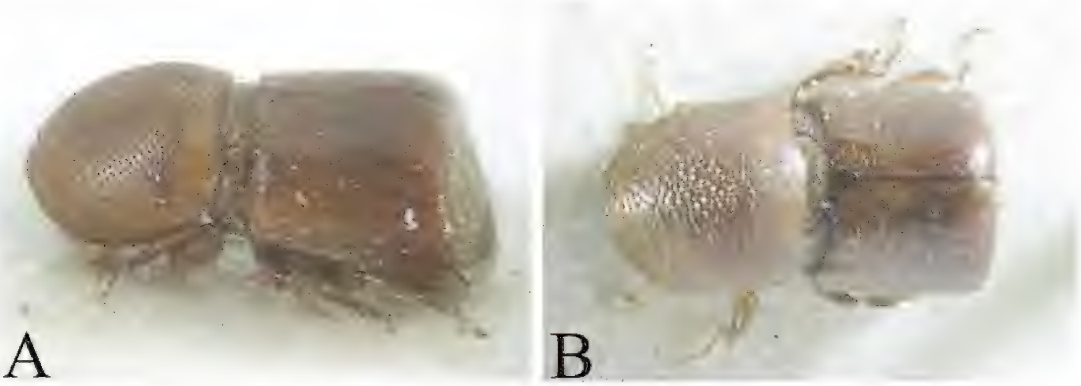


FIGURE 41. Lateral (A) and dorsal (B) views of *Xylosandrus subsimiliformis*, 2.8 mm, female paratype.

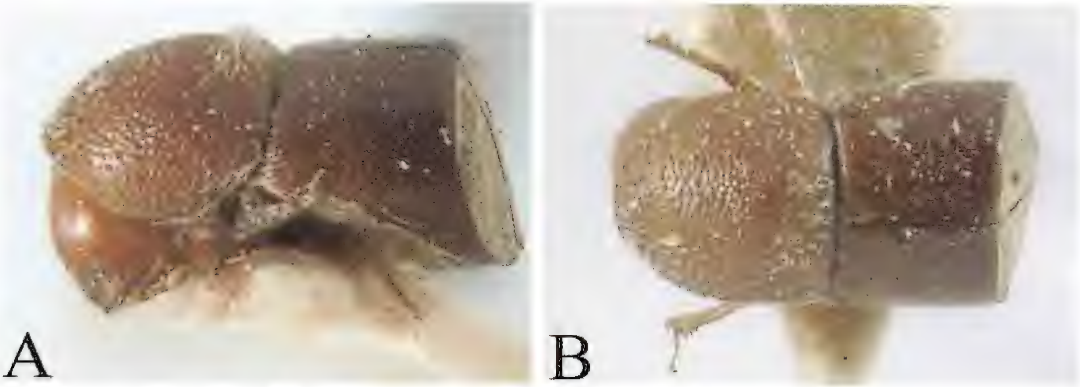


FIGURE 42. Lateral (A) and dorsal (B) views of *Xylosandrus subsimilis*, 2.6 mm, female paratype.

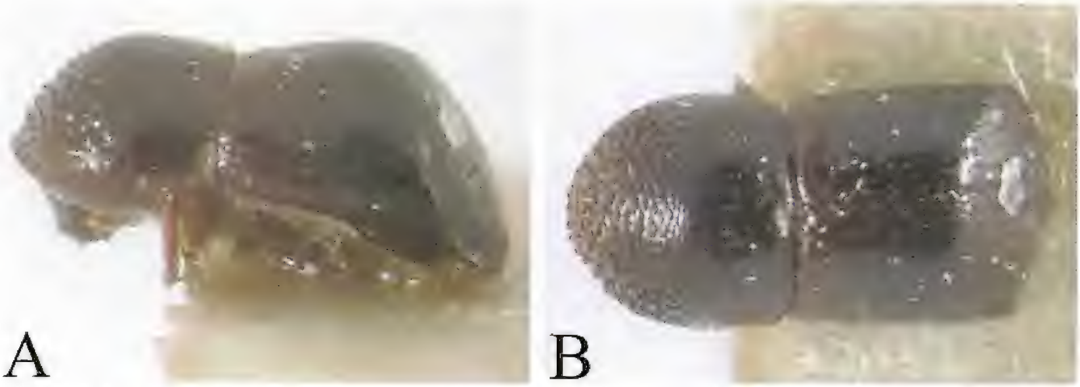


FIGURE 43. Lateral (A) and dorsal (B) views of *Xylosandrus terminatus*, 1.5–1.9 mm, female paratype.

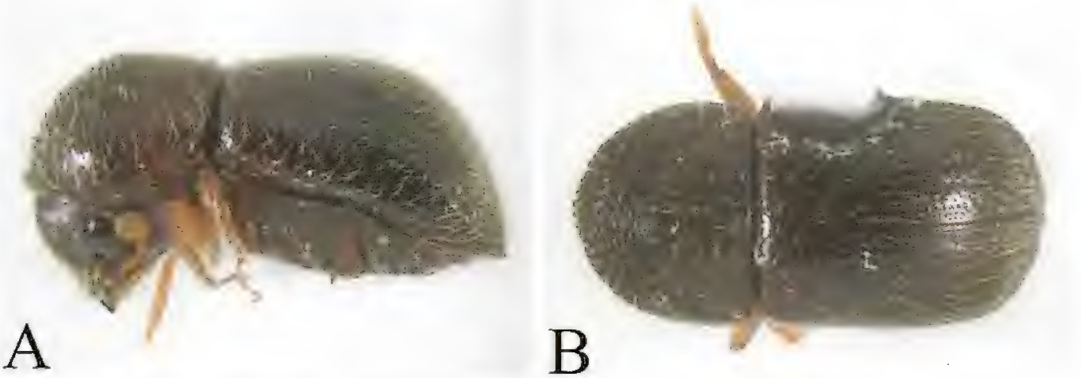


FIGURE 44. Lateral (A) and dorsal (B) views of *Xylosandrus woodi*, 2.3–2.4 mm, female paratype.

28 Aug–19 Oct 1991, Monteith and Janetzki, Pitfall and Intercept traps (1 ♀; RAB). **Oriental Region:** Indonesia: Java, 565 m., Bandjar, VII.32, L. G. E. Kalshoven (1 ♀; NHMW); Java, Boger, VIII-1964, N.L.H. Krauss, avocado branch (4 ♀; USNM); W. Java: 800 m Mount Gedeh, 7.1933, Leg. Kalshoven, Planta nutrix, *Eupartorium* (1 ♀; USNM). Malaysia: Koror, Palau Is. Apr 1953, J. W. Beardsley (1 ♀; USNM). Sri Lanka: Ceylon [Sri Lanka], Hantane, XII.1962, Dr. D. Calnaido (1 ♀; NHMW); Ceylon [Sri Lanka]: Perdadeiya, 11.VII.1914, A. Rutherford (2 ♀; USNM); Ceylon [Sri Lanka], Sabargamuva, 12.XI.1950, E. Judenko (1 ♀; NHMW); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S.L. Wood, Misc. hosts (4 ♀; USNM); Sri Lanka: Col. Dist., Labugama, 23 June 1975, S.L. Wood, collected from twigs (1 ♀; USNM); Sri Lanka: Mate. Dist., 48 km N Naula, 200 mtrs., 14 June 1975, S.L. Wood, Host: Rukaththana (1 ♀; USNM); Sri Lanka: Matte. Dist., 48 km, N Naula, 200 mtrs., 14 June 1975, S.L. Wood, collected from log (1 ♀; USNM); Sri Lanka: Mon. Dist., 8 km NW Bibile, 50 mtrs, 7 June 1975, S.L. Wood, collected from tree seedling (13 ♀; USNM); Sri Lanka: Mon. Dist., 8 km NW Bibile, 50 mtrs, 7 June 1975, S.L. Wood, collected from pole (2 ♀; USNM); Sri Lanka: Mon Dist. 8 km NW Bibile, 50 mtrs, 7 June 1975, S.L. Wood, collected from *Liana* (2 ♀; USNM); Sri Lanka: Rat. Dist., Ratnapura, Resthouse, 200-300 ft., 24-X-1976, black light, Collected by: G. F. Hevel, R.E. Dietz, W. S. Karunaratne, D. W. Balasooriya (1 ♀; USNM). Thailand: Thailand: Chiang Mai, 2.vii.72, R.A. Beaver, ex *Bauhinia variegata* (1 ♀; RAB); Thailand: Chiang Mai: Doi Inthanon, 5.viii.02, R.A. Beaver and K. Koivisto (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 13-14.iv.00, R. A. Beaver (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 12.x.93, R. A. Beaver, At light (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 1-3.I.2000, R.A. Beaver, M.T. (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 5.v.94, R.A. Beaver, At light (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 29–31.x.95, R.A. Beaver, M.T. (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 28.xi.02, R. A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 9.x.96, R.A. Beaver, ex mango twig (2 ♀; RAB); Thailand: Chiang Mai: Maerim, 5.x.96, R. A. Beaver, ex mango twig (1 ♀, 1 ♂; RAB); Thailand: Chiang Mai: Maerim, 21.ix.96, R. A. Beaver, ex mango twig (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 3.xii.96, R.A. Beaver, ex mango twig (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 16.x.96, R. A. Beaver, ex mango twig (1 ♂; RAB); Thailand: Chiang Mai: Maerim, 26.viii.99, R.A. Beaver, ex *Igall* sp. (1 ♀, 1 ♂; RAB); Thailand: Chiang Mai: Maerim, 23.vii.03, R.A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 10.xii.02, R. A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai: Maerim, 18.xi.03, R.A. Beaver, FIT (1 ♀; RAB); Thailand: Chiang Mai 300 m, Maerim, 16.I.92, R.A. Beaver (1 ♀; RAB); Thailand: Chiang Mai 300 m, Maerim, 15.I.92, R.A. Beaver (1 ♀; RAB).

Xylosandrus diversepilosus (Eggers)

Figure 21.

Xyleborus diversepilosus Eggers, 1941b:224. Holotype ♀: China, Prov. Fukien (Kuatun, 2300 m), 1.5.1938, L.J. Klapperich; ZMFK.
Xylosandrus diversepilosus (Eggers): Browne, 1963:55.

DIAGNOSIS.— Female 1.8–2.3 mm long; 2.1 times longer than wide. Body light brown; antennae and legs yellowish brown. Frons not visible on specimen examined. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their size. Pronotum with lateral costa, carinate. Procoxae not visible on specimen examined. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.2 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, without setae. Interstriae granulate, biseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. borealis* (Fig. 11) and *X. brevis* (Fig. 13). *Xylosandrus. diversepilosus* can be distinguished from these species by the following characters: declivital striae coarsely granulate, without setae; and interstriae granulate, with erect, hair-like setae, longer than twice the width of second declivital interstria.

Distribution.— **Oriental Region:** China (Fujian).

Hosts.— Unknown.

Specimens examined.— (1 ♀; 0 ♂) Type material: Holotype *Xyleborus diversepilosus* (♀; ZMFK).

Xylosandrus eupatorii (Eggers)

Figure 22.

Xyleborus eupatorii Eggers, 1940:140. Holotype ♀: Java (Tjibodas, G. Gedeh); Kalshoven Collection.
Xylosandrus eupatorii (Eggers): Schedl, 1964:213.

Diagnosis.— Female 1.8–2.1 mm long; 2.2 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Huler et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Huler et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined. Elytra 1.2 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. adherescens* (Fig. 7) and *X. germanus* (Fig. 24). *Xylosandrus eupatorii* can be distinguished from these species by the following characters: pronotum of equal length and width; pronotal disc glabrous, except for mycangial setae; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Distribution.— **Oriental Region**: Indonesia (Java).

Hosts.— "*Eupatorium tjibeureum*" (Java).

Specimens examined.— (1 ♀; 0 ♂) Type material: Cotype *Xyleborus eupatorii*: Java: Gedeh, 1700 M., VI.32, leg. H.R.A. Muller, *Eupatorium tjibeureum* (♀; NHMW).

Xylosandrus ferinus (Schedl)

Figure 23.

Xyleborus ferinus Schedl, 1936:31. Lectotype ♀: India: Travancore Mt. Estate, Tamil Nadu, VII.1934, S. A. Ran, on red gum; NHMW; designated by Schedl, 1979a:96.
Xylosandrus ferinus (Schedl): Browne, 1963:55.

Notes.— Schedl (1936) failed to designate a holotype in his original description of *X. ferinus* and subsequently designated a lectotype (Schedl 1979a).

Diagnosis.— Female 1.6–1.8 mm long; 2.2 times longer than wide. Body bicolored, pronotum distinctly lighter than elytra; pronotum light brown and elytra brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 8 socketed teeth; metatibial teeth not visible on specimens examined. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; insterstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, shorter than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 9), *X. discolor* (Fig. 20), *X. ferinus*, and *X. mesuae* (Fig. 30). *Xylosandrus ferinus* can be distinguished from *X. discolor* by the following characters: elytral disc gradually curving into declivity. *Xylosandrus ferinus* can be distinguished from *X. mesuae* by the following characters: larger species, 1.6–1.8 mm long; declivital striae without setae; and interstrial setae shorter than the width of second declivital interstriae. *Xylosandrus ferinus* can be distinguished from *X. arquatus* by the following characters: five striae visible on the elytral declivity; declivital striae without setae; and lighter color, with pronotum light brown and elytra brown.

Distribution.— **Oriental Region:** India (Tamil Nadu).

Hosts.— 'Red gum.'

Specimens examined.— (2 ♀; 0 ♂) Type material: Lectotype *Xyleborus ferinus* (♀; NHMW). Syntype *Xyleborus ferinus*: India: Travancore Mt. Estate, Tamil Nadu, VII.1934, S.A. Ran, on red gum (♀; NHMW).

Xylosandrus germanus (Blandford)

Figure 24.

Xyleborus germanus Blandford, 1894c:106. Syntypes ♀: Oyayama, Nikko, Subashiri, Kiga, Miyanashita: BMNH.

Xylosandrus germanus (Blandford): Hoffmann, 1941:38.

Xyleborus orbatus Blandford, 1894c:123. Holotype ♀: Kurigahara, Japan; BMNH. Synonymy: Choo, 1983:100.

Notes.— Browne (1963) wrongly lists *X. germanus* as the type species for *Xylosandrus*.

Diagnosis.— Female 1.9–2.5 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11–12 socketed teeth; metatibiae with 12–13 socketed teeth. Elytra 1.1 times longer than wide; 1.1 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. adherescens* (Fig. 7) and *X. eupatorii* (Fig. 22). *Xylosandrus germanus* can be distinguished from these species by the following characters: pronotum longer than wide; and pronotal disc evenly pubescent, not glabrous.

DISTRIBUTION.— **Nearctic Region (Introduced):** Canada (British Columbia, Ontario, Quebec), United States (Connecticut, Delaware, Florida, Illinois, Indiana, Kentucky, Maine, Massachusets, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, Rhode Island, Virginia, West Virginia). **Oceania (Introduced):** Hawaiian Islands. **Oriental Region:** China (Anhui, Fujian, Shanxi, Xizang [Tibet], Yunnan), Japan, Ryukyu Islands, Taiwan, Vietnam. **Palearctic Region:** Austria (Introduced), Belgium (Introduced), France (Introduced), Germany (Introduced), Italy (Introduced), Korea, Switzerland (Introduced), Yugoslavia (Introduced).

HOSTS.— *Abies fabric* (Masters) Craib, *A. pectinata* Poir., *Acer* L. spp., *A. platanoides* L., *A. pseudoplatanus* Falk., *Alnus glutinosa* (L.) Gaertn., *Alnus* Mill. sp, , *Betula verrucosa* Ehrh., *Carpinus betulus* L., *C. laxiflora* (Siebold and Zucc.) Blume, *Carya* Nutt. sp., *Cassia siamea* Lam., *Castanea crenata* Siebold and Zucc., *Castanopsis* (D. Don) Spach sp., *Celtis tenuifolia* Nutt., *Chamaecyparis obtuse* Siebold and Zucc., *Cleyera japonica* Siebold and Zucc., *Cornus florida* L., *Diospyros kaki* Thunb., *Fagus crenata* Blume, *Fagus multinervis* Nakai, *F. sylvatica* L., *Fraxinus* L. spp., *Juglans regia* L., *Juglans* L. sp., *Myrica carolinensis* Mill., *Myrica* L. sp., *Lindera erythrocarpa* Makino, *Liriodendron tulipifera* L., *Machilus* Nees sp., *Morus* L. spp., *Nyssa aquatica* L., *Picea abies* (L.) K. Harst., *P. excelsa* Link, *Pinus densiflora* Siebold and Zucc., *P. pentaphylla* Carrière, *P. strobes* L., *Pinus* L. sp., *Prunus avium* (L.) L., *P. cerasus* L., *Prunus serotina Ehrh.*, *Prunus* L. spp., *Pyrus serotina* Rehder, *Pyrus* L. sp., *Rhus chinensis* Mill., *Quercus rubra* L., *Q. sessiliflora* Salisb., *Quercus* L. spp., *Robinia pseudoacacia* L., *Schima superba* Gardn. and Champ., *Styrax obassia* Siebold and Zucc., *S. japonicus* Siebold and Zucc., *Taxodium distichum* Rich., *Ulmus effuse* Willd., *Ulmus* L. spp., *Vitis* L. sp., "young chestnut" (Japan), *Ziziphus jujuba* Mill.

SPECIMENS EXAMINED.— (66 ♀; 6 ♂) OTHER MATERIAL: **Nearctic Region:** United States: Indiana: Turkey Run St. Park, VI-10-1967, L. and C.W.O'Brien (1 ♀; USNM); Indiana: W. Lafayette, McCormick Woods, V.26-1968, Collectors L. and C.W. O'Brien (1 ♀;USNM); IND., W. Lafayette, Tippercanoe Co., 12 Apr. 1981, M. and N. Deyrup, in pan trap below Malaise trap (2 ♀; RAB); Maryland: Takoma Park, Montgomery Co., 17-IV-1969, W.H. Tyson (1 ♀; USNM); North Carolina: McDowell Co., 10.20.1976, B.C. Weber collector (1 ♂; USNM); North Carolina: McDowell Co., 7-21 1977, B. C. Weber collector (1 ♀, 1 ♂; USNM); North Carolina: McDowell Co., 10-19 1976, B.C. Weber collector (2 ♀; USNM); North Carolina: McDowell Co., 10.20.1976, B.C. Weber collector (9 ♀; USNM); North Carolina: Raleigh, 25.6.63, *Prunus serotina* (1 ♀; NHMW); New Jersey: Norwood, Apl 11 1944, Schott, from branches of *Myrica carol* (6 ♀; USNM); New Jersey: Princeton, 2 June 1971, R.J. Gouger, *Fagus sylvatica* (4 ♀; USNM); New York: Kingston, Jun 8, 1939, Esselbaugh, H.R. Dodge Collection (1 ♀; USNM); New York: New Rochelle, IV.20.1932, L. Lacey collector (3 ♀; USNM); Ohio: Chillicothe, 28-VI-50, *Liriodendron tulipifera* (3 ♀; USNM); Ohio: Moreland Hills, 3.VIII.1981, W.V. Miller (1 ♀; CAS); Virginia: Albemarle Co., Ivy ex *Vitis*, cane tunnels, 29 Apr 1983, D.G. Pfeiffer coll. (2 ♀; USNM). **Oriental Region:** China: S. China: Fukien, Shaowu, Tachulan, V.14.1942, T. Maa (2 ♀; CAS). Japan: Japan: III-1917, Van Dyke Collection, in trunk of young chestnut (1 ♀; CAS); Japan, Hokkaido, Gamushi, VI.9.1956, Akira Nobuchi (2 ♀; USNM); Japan: Honshu, Higashiaraya, Kushibiki-machi, Yamagata Pref., 13.Vi.1996, K. Domon leg., Host tree: *Pyrus serotina* Rehder (1 ♀, 2 ♂; RAB); Japan: Kyushu, Shiiya-touge Pass, Miyazaki-Kumamoto Pref., 25.Vi.1994, H. Goto leg. (1 ♀; RAB); Japan: Matsukawa, 27-VII-1980, S.L. Wood (1 ♀; USNM); Japan: Tamagowa, 29-VII-1980, S.L. Wood, *Fagus* *cranatus* (6 ♀; USNM); Japan: Tokyo, Mt. Takao, IX.22.1950, Akira Nobuchi (2 ♀; USNM). Thailand: Thailand: Chiang Mai: Doi Suthep, 7.viii.02, R.A. Beaver, K. Koivisto (2 ♀; RAB). **Palearctic Region:** Germany: Germania (Hessen) 28.8.52, Darmst-Kranichst, Geishecke, leg. F. Groschike, *Quercus* (1 ♂; NHMW, 1 ♂; BMNH); IGB–Sengscheid, SAAR, Wald, 18.6.90, leg. Mosbacher (4 ♀; RAB). Switzerland: Helvetia, Arlesheim, 1988, In traps (2 ♀; RAB). **Oceania:** Hawaiian Islands: USA: HI: O'ahu I., N. Halawa Valley, NW of Honolulu, 390 m, 21°25′N, 157°51′W, 11-29.VI.1991, FMHD#91-4, Met. Polym.-Psidium-Hibiscus mixed nat./exotic forest, A. Newton and M. Thayer, #869, window trap (4 ♀; FMNH).

Xylosandrus hirsutipennis (Schedl)

Figure 25.

Xyleborus hirsutipennis Schedl, 1961b:144. Holotype ♀: Madagascar, Perinet, Montagne d'Ambre, Antanditra: IRSM.
Xylosandrus hirsutipennis (Schedl): Wood and Bright, 1992:796.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination."

DIAGNOSIS.— Female 1.9–2.2 mm long; 2.3 times longer than wide. Body brown to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 7 socketed teeth; metatibiae with 7 socketed teeth. Elytra 1.3 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae granulate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. crassiusculus* (Fig. 16). Both species have a declivital face that is matte in appearance due to densely, finely, and confusedly granulate striae and interstriae. *Xylosandrus hirsutipennis* can be distinguished from *X. crassiusculus* by the following characters: frons punctate; pronotum with a lateral carina; pronotal disc glabrous, except for mycangial setae; elytral disc uniseriate punctate; five striae visible on elytral declivity; and declivital striae and interstriae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

DISTRIBUTION.— **Afrotropical Region:** Madagascar.

HOSTS.— *Cassipourea* Aubl. sp., *Ficus soroceoides* Baker var. *macrophlebia* H. Perrier, *Harungana madagascariensis* Poir., *Psychotria* L. sp., *Urophyllum lyallii* Baker, *Vernonia* Schreb. sp.

SPECIMENS EXAMINED.— (3 ♀; 1 ♂) TYPE MATERIAL: Paratypes *Xyleborus hirsutipennis*: Madagascar, Perinet, 21.XI.1952, Dr. K.E. Schedl (2 ♀; NHMW); Madagascar, Montagne d'Ambre, 7.XII.1952, Dr. K.E. Schedl (1 ♂; NHMW); Madagascar, Montagne d'Ambre, 5.XII.1952, Dr. K. E. Schedl (1 ♀; NHMW).

Xylosandrus huleri **Dole and Cognato, sp. nov.**

Figure 26.

Description.— Female (Fig. 26): Body oval, 2.4–2.7 mm long, 2.0 times longer than wide, bicolored, with pronotum and elytral apices dark brown, dorsal ⅓ and lateral ⅔ of elytra yellowish brown, ventral side and appendages dark brown. Frons convex, coriaceous, sparsely punctate between eyes, long erect hair-like setae originating from punctures, weak ridge at middle of frons just above epistoma. Epistoma with dense row of long and short hair-like setae along lower margin. Eyes emarginate. Antennal funicle 5-segmented, scape and funicle with spare, short, hair-like setae; club obliquely truncate, first segment sclerotized, forming a circular costa (type 1, Hulcr et al. 2007), circular costa closed posteriad, oblique part of club densely pubescent, second segment not corneous; posterior face of club covered entirely by first segment (type 1, Hulcr et al. 2007). Pronotum 0.9 times longer than wide, rounded dorsally (type 1, Hulcr et al. 2007), widest about one-half pronotal length from base, anterior half broadly rounded and then tapering slightly toward apex, basal angles rounded, anterior margin with 4–6 asperities; anterior slope densely asperate, asperities smallest at summit and increasing in size toward anterior margin; disc moderately punctate, lacking a patch of denser punctures medially at base, background sculpture finely granulate; lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007), lateral costa extending approximately two-thirds pronotal length, lateral carina absent; pronotal vestiture of long and short, moderately appressed, hair-like setae. Scutellum triangular, yellowish-brown to dark brown, flush with surface of elytra. Elytra 1.2 times longer than wide, 1.4 times as long as pronotum, shining, parallel-sided on basal two-thirds and then broadly rounded toward apex. Striae not impressed, shallowly and regularly punctate, long erect hair-like setae originating from punctures. Interstriae twice the width of striae, finely punctate, confused, long (1.5–2 times width of interstria) and short (less than width of interstria) erect hair-like setae originating from punctures. Declivity commencing behind mid-point of elytra, gradually separating from disc; lateral margins carinate to 7th interstriae. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 7–8 socketed teeth; metatibiae with 8 socketed teeth. Abdominal ventrites evenly punctured, punctures with long, erect, hair-like setae.

Specimens examined.— (4 ♀; 0 ♂) Type material: Holotype ♀: Papua New Guinea, Chimbu, Mu Village, March 2006, 1600 m asl. Hulcr and Coganto coll. *Ficus mollior*. Vila 1462. In MSU. Paratypes ♀: Papua New Guinea, Chimbu, Mu Village, March 2006, 1600 m asl. Hulcr and Coganto coll. *Ficus mollior*. Vila 1462. One paratype in FICB. Three paratypes in MSU. One paratype female was used for DNA extraction, and remains are vouchered at MSU.

Male: Unknown.

Etymology.— This species is named for Jiri Hulcr (Michigan State University), who collected the type series and whose collecting efforts have contributed greatly to our knowledge of the tropical scolytine fauna.

Diagnosis.— This species can be readily distinguished from all other known *Xylosandrus* species by its distinct color pattern, with testaceous patches on the elytra basally and laterally.

Distribution.— **Australian Region:** Papua New Guinea.

Hosts.— *Ficus mollior* Benth.

Discussion.— This species is known from a single collecting event. Specimens were collected at the same locality, but from galleries in several host trees. This species is mycocleptic and has been found in association with and stealing ambrosial fungus from *Xylosandrus rotundicollis*. Phylogenetic analysis places it as sister to the Australian species, *X. queenslandi*.

Xylosandrus jaintianus (Schedl)

Figure 27.

Xyleborus jaintianus Schedl, 1967:161. Holotype ♀: Shillong, Assam, C.F.C. Beeson, 22.V.1925; NHMW.
Xylosandrus jaintianus (Schedl): Wood and Bright, 1992:796.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination."

DIAGNOSIS.— Female 3.0 mm long; 2.0 times longer than wide. Body brown; antennae and legs same color as body. Frons rugose, with distinct median keel between eyes. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Huler et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mestonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic (type 0, Huler et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 11–12 socketed teeth. Elytra 1.1 times longer than wide; 1.1 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity with depressed areas on each side of raised interstriae, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beesoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 20), and *X. subsimiliformis* (Fig. 41). *Xylosandrus jaintianus* can be distinguished from these species by the following characters: first and second declivital interstriae elevated toward apex, with depressed areas on each side of raised interstriae; frons rugose with a distinct median keel.

DISTRIBUTION.— **Oriental Region:** Burma, India (Assam). **Palearctic Region:** Nepal.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (4 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xyleborus jaintianus* (♀; NHMW). Paratype *Xyleborus jaintinaus*: N.E. Burma: Kambaiti, 7000ft., 23/5/1934, R. Malaise (♀; BMNH).

OTHER MATERIAL: **Palearctic Region:** Nepal: Nepal-Himalaya: Annapurna mts. N-Pokhara, Madi-Khola-Tal, 1850m, 2.v.1996, leg. O. Jäger (1 ♀; RAB); Nepal, Kali Gandaki Tai 2 km SO Narcheng oberth. Rele Khola, HO-Hang, 2300 m, N28°30'40", E83°41'33", 25.v.2001, leg. O. Jäger (1 ♀; RAB).

Xylosandrus mancus (Blandford)

Figure 28.

Xyleborus mancus Blandford, 1898:428. Holotype ♀: Ceylon, E. E. Green; BMNH.
Apoxyleborus mancus (Blandford): Wood 1980:90.
Xylosandrus mancus (Blandford): Wood 1984:229.
Xyleborus abruptus Sampson, 1914:388. Syntypes ♀: Seychelles, Mahe: high forest of Morne Blanc, and Cascade Estate; BMNH. Synonymy: Schedl, 1951:51.
Xyleborus mancus formosanus Eggers, 1930:186. Holotype ♀: Formosa: Taihoku; FRI. Synonymy: Schedl, 1952:61.

NOTES.— This species was first included in *Xylosandrus* when Wood (1984) synonymized *Apoxyleborus* with *Xylosandrus*.

Diagnosis. Female 2.9–3.3 mm long; 1.2–1.4 times longer than wide. Body yellowish brown to brown; elytra darker brown at apex and declivity; legs and antennae the same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming circular costa; segment one covering entire posterior face. Of approximately equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; mesotibiae with 11 socketed teeth; metatibiae with 12 socketed teeth. Elytra 1.2 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate, with carina extending beyond 7th interstriae, forming a circumdeclivital ring. Four striae visible on declivity. Striae punctate, without setae. Interstriae granulate, without setae.

This species is one of two *Xylosandrus* with the margin of the elytral declivity with a carina or rim of granules that extends beyond the 7th interstriae, forming a circumdeclivital ring: *X. amputatus* (Fig. 8) and *X. mancus*. *Xylosandrus mancus* can be distinguished from *X. amputatus* by the following characters: 2.9–3.3 mm long; 1.2–1.4 times as long as wide; declivtial striae with a row of large, shallow punctures, arranged in a somewhat wavy line; and declivital interstriae shining, not densely granulate.

Distribution.— **Afrotropical Region:** Madagascar, Mauritania, Seychelles Islands, Tanzania. **Oriental Region:** China (Gansu, Xizang [Tibet]), India (Maharashtra, Tamil Nadu), Indonesia (Java, Sumatra), Japan, Malaysian Peninsula, Philippines, Sri Lanka, Taiwan, Thailand, Vietnam.

Hosts.— *Adenanthera pavonina* L., *Albizia* Benth. sp., *Anacardium occidentale* L., *Aphanamixis rohituka* Pierre, *Artocarpus dadah* Miq., *Brackenridgea hookeri* (Planch.) A. Gray, *Buchanania lanzan* Spreng., *B. latifolia* Roxb., *Butea frondosa* Wall., *Calophyllum inophyllum* L., *Cassia fistula* L., *Cordia dichotoma* G. Forst., *Cordia myxa* L., *Dalbergia latifolia* Roxb., *Dryobalanops aromatica* Gaertn., *D. oblongifolia* Dyer, *Gomphia serrata* (Gaertn.) Kanis, *Grewia paniculata* Roxb., *Hibiscus macrophyllus* Roxb., *Hopea beccariana* Burck, *H. ferrea* Heim, *Hullettia dumosa* King, *Khaya senegalensis* Juss., *Litsea megacarpa* Gamble, *Mangifera indica* L., *Melanorrhoea* Wall. sp., *Nephelium lappaceum* L., *Palaquium gutta* Burk., *Pometia pinnata* J. R. Forst. and G. Forst., *Quercus* L. sp., *Shorea bracteolata* Dyer, *S. leprosula* Miq., *S. macroptera* Dyer, *S. sumatrana* (Slooten) Desch, *Styrax benzoin* Dryand., *Swietenia macrophylla* King, *S. mahagoni* (L.) Jacq., *Tectona grandis* L., *Theobroma cacao* L., *Toona sureni* Merrill., *Tristania whiteana* Griff., *Vateria copallifera* (Retz.) Alston, *Vitex pubescens* Vahl.

Specimens examined.— (69 ♀; 2 ♂) Type material: Holotype *Xyleborus mancus* (♀; BMNH).

Other material: **Afrotropical Region:** D.O. Africa (1 ♀; NHMW). Madagascar: Madagascar, Ambila, 28.XI.1952, K.E. Schedl (1 ♀, 1 ♂; NHMW). Seychelles: Seychelles: P.R. Dupont, 1915, attacking Cashew (3 ♀; BMNH). **Oriental Region:** Indonesia: Java: Kediri Forest, II.1925, L.G.E. Kalshoven (2 ♀; USNM); Java: Kediri, III.1925, L.G.E Kalshoven (1 ♀; NHMW). Japan: Japan: Kagoshima Pref., Tarumizuy, Oonohara, Broadleaf forest, 425 m, 14 May 2001, Yoshikazu Sato coll., ex. ETOH-baited trap (2 ♀; MSU); Japan: Kagoshima Pref., Tarumizuy, Oonohara, Broadleaf forest, 425 m, 3 July 2001, Yoshikazu Sato coll., ex. ETOH-baited trap (1 ♀; MSU). Malaysia: Sarawak, Bako National Park, 29 Oct–2 Nov 1998, 50 m, B. Jordal coll. (1 ♀; MSU); Malaya, Selangor, Kepong, 8.IV.1934, Selangor Mus., ex. *Styrax benzoin* (1 ♀; NHMW); Selagor, Kajang, ex *Clenderai* [*Clerodendron*?], 5. XII.1948, F.G. Browne (3 ♀; USNM). Philippine Islands: Manila, Philippine Islands, Colln PC, McGregow (1 ♀; USNM); Philippine Islands: Puerto Princesa, Palawan Is., sea level, 2nd growth forest, IV.29.47, H. Hoogstraal leg. (1 ♀; FMNH). Singapore: Singapore, Bukit Timah, 50 m, 25–27 Oct 1998, B.H. Jordal coll., *Cinnamomum* (1 ♀; MSU). Sri Lanka: Sri Lanka: Bad. Dist., Buttala, 5 June 1975, S.L. Wood, collected from liana (5 ♀; USNM); Sri Lanka: Bad. Dist., Butatala, 5 June 1975, S.L. Wood, collected from pole (8 ♀, 1 ♂; USNM); Sri Lanka: Bat. Dist., Unnichchai, 9 June 1975, S.L. Wood, collected from liana (2 ♀; USNM); Ceylon [Sri Lanka]: Col. Dist. Tunmodera, 200 ft, 17-XI-1970, O.S. Flint, Jr. (2 ♀; UISNM); Sri Lanka: Gal. Dist., Kanneliya, 250 mtrs., 23 May 1975, S.L. Wood, Collected from pole (9 ♀; USNM); Ceylon [Sri Lanka]: Hantane, XII.1962, D. Calnaido (1 ♀; NHMW); Ceylon [Sri Lanka]: Kan. Dist., Kandy, 1-15 March 1971, Piyadasa and Somapala (4 ♀; USNM); Ceylon [Sri Lanka]: Kan. Dist., 5 mi NW Mahiyangana, 30 Mar-9 Apr 1971, P. and P. Spangler (2 ♀; USNM); Sri Lanka: Keg. Dist., Kitulgala, 200 m, 30 May 1975, S.L. Wood, host: *Osbeckia aspera* (1 ♀; USNM); Sri Lanka: Matte. Dist., 5 km SE Naula, 200 mtrs, 14 June 1975, S.L. Wood, misc. hosts (4 ♀; USNM); Sri Lanka: Matte. Dist., 5 km SE Naula, 200 mtrs, 14 June 1975, S.L. Wood, collected from *Liana* (1 ♀; USNM); Sri Lanka: Mon. Dist. 8 km NW Bibile, 50 mtrs, 7 June 1975, S.L. Wood, collected from pole (5 ♀; USNM); Sri Lanka: Mon. Dist., Buttala, 50 mtrs, 6 June 1975, S.L. Wood, collected from pole (1 ♀; USNM); Sri Lanka: Pol. Dist. 32 km N Polonnaruwa, 11 June 1975, S.L. Wood, collected from pole (1 ♀; USNM); Sri Lanka: Rat. Dist. Gilimale, 17 May 1975, S.L. Wood, host: *Myristica dactyloides* (1 ♀; USNM); Ceylon [Sri Lanka]: Rat. Dist., Uggaalkaltota 350 ft., irrigation bungalow, 31 Jan–8 Feb 1970, Davis and Rowe (1 ♀; USNM); Ceylon [Sri Lanka], Sabagamuva, Millawitiya Est., 3-10.Vii.1956, E. Judenko (1 ♀; NHMW).

Xylosandrus mediocris (Schedl)

Figure 29.

Xyleborus mediocris Schedl, 1942a:185. Lectotype ♀: Malaya, N.S. Pasoh Forest Reserve, 12-II-1938, ex *Shorea dasyphylla*; NHMW.
Xylosandrus mediocris (Schedl): Browne, 1963:55.

Diagnosis.— Female 1.4 mm long; 2.3 times longer than wide. Body brown; antennae and legs yellowish brown. Frons not visible on specimen examined. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae not visible on specimen examined. Pro-, meso- and metatibial teeth not visible on specimen examined. Elytra 1.3 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae uniseritae punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. adherescens* (Fig. 7), *X. eupatorii* (Fig. 22), and *X. germanus* (Fig. 24). *Xylosandrus mediocris* can be distinguished from these species by the following characters: 1.4 mm long; pronotum of equal length and width; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than the width of second declivital interstriae.

Distribution.— **Oriental Region:** Malaysia.

Hosts.— *Dipterocarpus cornutus* Dyer, *Shorea dasyphylla* Foxw.

Specimens examined.— (1 ♀; 0 ♂) Type material: Lectotype *Xyleborus mediocris* (♀; NHMW).

***Xylosandrus mesuae* (Eggers)**
Figure 30.

Xyleborus mesuae Eggers, 1930:182. Holotype ♀: Bengal (Kalimpong), Aug. 1910 on *Mesua ferra*; FRI.
Xylosandrus mesuae (Eggers): Browne, 1963:55.

DIAGNOSIS.— Female 1.1–1.3 mm long; 2.2 times longer than wide. Body bicolored, pronotum distinctly lighter than elytra; pronotum light brown and elytra dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 6 socketed teeth; metatibiae with 8 socketed teeth. Elytra 1.3 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae uniseriate, very finely punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of four bicolored *Xylosandrus* with the pronotum distinctly lighter than the elytra: *X. arquatus* (Fig. 9), *X. discolor* (Fig. 20), *X. ferinus* (Fig. 23), and *X. mesuae*. *Xylosandrus mesuae* can be distinguished from *X. discolor* by the following characters: elytral disc gradually curving into declivity. *Xylosandrus mesuae* can be distinguished from *X. arquatus* and *X. ferinus* by the following characters: 1.1–1.3 mm long; declivital striae with setae; declivital interstriae with erect, hair-like setae, longer than the width of second declivital interstriae.

DISTRIBUTION.— **Australian Region:** Papua New Guinea. **Oriental Region:** India (Bengal, Uttar Pradesh), Sri Lanka.

HOSTS.— *Dipterocarpus zeylanicus* Thwaites., *Macaranga* Thou. sp., *Mesua ferrea* L., *Osbeckia aspera* Benth., *Shorea robusta* Roth.

SPECIMENS EXAMINED.— (102 ♀; 1 ♂) TYPE MATERIAL: Paratype *Xyleborus mesuae*: Bengal, Kalimpong on *Mesua ferrea* (♀; NHMW).

OTHER MATERIAL: **Australian Region:** Papua New Guinea: Papua New Guinea, Lae, 15 km S Lae, 100 m, 13.2.2003, B. Jordal and A. Sequeira leg. ex *Macaranga* petoles (3 ♀; RAB). **Oriental Region:** Sri Lanka: Ceylon [Sri Lanka]: 10-16.VII.1956, Sabargamuva, Millawitiya Est., E. Judenko (1 ♀; NHMW); Sri Lanka: Col Dist. Labugama, 23 June 1975, S.L. Wood, collected from legume tree (2 ♀; USNM); Sri Lanka: Col. Dist. Labugama, 23 June 1975, S.L. Wood, collected from twigs (64 ♀; USNM); Sri Lanka: Col. Dist. Labugama, 23 June 1975, S.L. Wood, host: *Dipterocarpus zeylanicus* (25 ♀, 1 ♂; USNM); Sri Lanka: Keg. Dis. Kitulgala, 200 m, 30 May 1975, S.L. Wood, host: *Osbeckia aspera* (6 ♀; USNM).

***Xylosandrus metagermanus* (Schedl)**
Figure 31.

Xyleborus metagermanus (Schedl), 1951: 58. Holotype ♀: U. Dihing Res., Lakhimpur Assam, 6. VIII. 1931, ex *Gmelina arborea*, C. F. C. Beeson; NHMW.
Xylosandrus metagermanus (Schedl): Browne, 1963: 55.

DIAGNOSIS.— Female 1.8 mm long; 2.0 times longer than wide. Body light brown to brown; antennae and legs same color as body. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 5 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimen examined. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. mixtus* (Fig. 32). *Xylosandrus metagermanus* can be distinguished from *X. mixtus* by the following characters: 1.8 mm long; six striae visible on declivity; declivital striae without setae; declivital interstriae uniseriate granulate.

Distribution.— **Oriental Region:** India (Assam).

Hosts.— *Gmelina arborea* Roxb.

Specimens examined.— (1 ♀; 0 ♂) Type material: Holotype *Xyleborus metagermanus* (♀; NHMW).

Xylosandrus mixtus (Schedl), new combination

Figure 32.

Xyleborus mixtus Schedl, 1979b:108. Holotype ♀: Papua, Butolo, Morobe Distr., Upper Monki, L.A., 16.3.1973, sticky trap Nr. 1604, F.R. Wylie and P. Shanahan; NHMW.
Amasa mixtus (Schedl): Wood and Bright, 1992:683.

Notes.— This species was first included in *Amasa* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination."

Diagnosis.— Female 2.6–2.7 mm long; 2.4 times longer than wide. Body light brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae narrowly, but completely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 9 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.4 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with erect, hair-like setae, more than twice as long as width of second declivital interstriae.

This species is morphologically similar to *X. metagermanus* (Fig. 31). *Xylosandrus mixtus* can be distinguished from *X. metagermanus* by the following characters: 2.6–2.7 mm long; five striae visible on elytral declivity; declivital striae with semi-appressed, hair-like setae; declivital interstriae multiseriate granulate.

Distribution.— Australian Region: New Guinea.

Hosts.— Unknown.

Specimens Examined.— (1 ♀; 0 ♂) Type material: Holotype *Xyleborus mixtus* (♀; NHMW).

Xylosandrus monteithi Dole and Beaver

Figures 33–34.

Xylosandrus monteithi Dole and Beaver, 2008. Holotype ♀: AUSTRALIA, Queensland, Palmerston, Henrietta Cr., 550m, ex unknown tree, 22.1.2000 (B. Jordal). In QMB (Accession # T144402).

Diagnosis.— Female 3.0–3.4 mm long; 2.1 times longer than wide. Body dark brown or blackish, base of pronotum and elytra lighter brown, ventral side and appendages yellowish brown. Frons reticulate with coarse punctures. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of erect and semi-appresssed long hair-like setae; pronotal disc densely setose, setae as dense as on anterior pronotum. Pronotum lacking a dense patch of setae at base of pronotum. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin, meso- and metatibiae with 7–9 socketed teeth. Elytra 1.2 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate, becoming granulate toward declivity. Elytral disc gradually curving into declivity. Declivity convex, lateral margins rounded, without a carina or a row of tubercles or serrations. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with semi-appressed, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. rotundicollis* and *X. russulus*. *Xylosandrus monteithi* can be distiniguished from these two species by the following characters: Basal pronotum lacking a dense patch of setae; declivital striae with semi-appressed, hair-like setae, longer than the width of second declivital interstriae. *Xylosandrus monteithi* may also be confused with *X. woodi*, but the later species has small tubercles marking the lateral declivital margin.

Distribution.— Australian Region: Australia (Queensland).

Hosts.— Unknown.

Specimens examined.— (1 ♀; 1 ♂) Type material: Paratype *Xylosandrus monteithi*: Australia, Queensland, Palmerston, Watchua Falls, Jan. 2000, 550 m, ex unknown tree, 24.1 B. Jordal leg (♀; MSU). Allotype *Xylosandrus monteithi*: Australia, Queensland, Palmerston, Watchua Falls, Jan. 2000, 550 m, ex unknown tree, 24.1 B. Jordal leg. (♂; MSU).

Xylosandrus morigerus (Blandford)

Figure 35.

Xyleborus morigerus Blandford, 1894a:264. Syntypes ♀: probably New Guinea; BMNH.

Xylosandrus morigerus (Blandford): Reitter, 1913:83.

Xyleborus coffeae Wurth, 1908:199. Syntypes ♀: Java; type location unknown. Synonymy: Strohmeyer, 1910:86.

Xyleborus luzonicus Eggers, 1923:174. Lectotype ♀: Mt. Makiling, Insel Luzon, Philippinen; USNM.

Xylosandrus luzonicus (Eggers): Browne, 1963:55. Synonymy: Wood, 1974:287.

Xyleborus difficilis Eggers, 1923:174. Lectotype ♀: Java, Hagedorn coll., 1915; USNM.

Xylosandrus difficilis (Eggers): Browne, 1963:55. Synonymy: Synonymy Bright and Skidmore 1997:4, 169.

Xyleborus abruptoides Schedl, 1955:298. Holotype ♀: Fiji: Viti Levu, Navai Mill, near Nandarivatu, 2500 ft., 15.IX.1938, beating shrubbery; BPBM.
Xylosandrus abruptoides (Schedl): Browne, 1963:55. Synonymy (= *Xylosandrus difficilis*) Beaver 1995:17.

DIAGNOSIS.— Female 1.5–2.0 mm long; 2.1 times longer than wide. Body light to dark brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with a lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 8–10 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face steep and abruptly separated from disc. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with erect hair-like setae, shorter than the width of second declivital interstriae. Interstriae punctate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. derupteterminatus* (Fig. 18) and *X. terminatus* (Fig. 43). *Xylosandrus morigerus* can be distinguished from these species by the following characters: elytral declivity convex; six striae visible on declivity; declivital striae with setae; and declivital interstriae uniseriate punctate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

DISTRIBUTION.— **Afrotropical Region:** Gabon, Madagascar, Mauritius Islands, Zaire. **Australian Region:** Australia (Queensland), New Britain Island, New Guinea, Solomon Islands. **Neotropical Region:** Brazil, Colombia, Costa Rica, Ecuador (Santa Cruz in Galapagos Islands), Honduras, Mexico (Campeche, Chiapas, Oaxaca, Tabasco, Varacruz), Panama, Puerto Rico, Tobago, Venezuela. **Oceania:** Fiji Islands, Hawaiian Islands, Micronesia, Samoan Islands, Tonga (Vava'u). **Oriental Region:** India (Bengal, Tamil Nadu), Indonesia (Borneo, Celebes, Java, Sumatra, Timor), Malaysia (Sarawak), Philippines, Sri Lanka, Taiwan, Vietnam. **Palearctic Region (Introduced):** Austria, Czechoslovakia, United Kingdom, France, Italy, Jordan, Lebanon.

HOSTS.— *Acacia gaumeri* S.F. Blake, *Acalypha* L. sp., *Actinophora fragrans* Wall., *Adenanthera pavonina* L., *Albizia falcate* (L.) Backer, *A. glauca* Benth., *A. procera* Benth, *Albizia* Durazz. sp., *Alseis yucatanensis* Standl., *Altingia excelsa* Noronha, *Arthrophyllum diversifolium* Blume, *Amomum* L. sp., *Aspidosperma* Mart and Zucc. sp., *Astronium graveolens* Jacq., *Bixa orellana* L., *Boehmeria* Jacq. sp., *Bridelia* Willd. sp., *Brosimum alicastrum* Sw., *Bursera simaruba* (L.) Sarq., *Butea monosperma* Kuntze, *Calamus* L. sp., *C. caesius* Blume, *Calophyllum brasiliense* Camb., *Camellia sinensis* Kuntze, *C. thea* Link., *C. theifera* Dyer, *Cassia multijuga* Rich., *Castanea argentea* Blume, *Castanopsis* (D. Don.) Sprach. sp., *Cattleya* Lind. sp., *Cedrela odorata* L., *Cedrela* P. Browne sp., *Cecropia obtusifolia* Bertol., *Ceiba pentandra* (L.) Gaertn., *Centrosema plumieri* Benth., *Cecropia* Loefl. sp., *Chrysophyllum cainito* L., *Cinchona* L. sp., *Claoxylon polot* Merr., *Clidemia hirta* Don., *Cocos nucifera* L., *Coffea arabica* L., *Coffea excelsa* Cheval., "*C. hybrida*" (Java: Schedl 1963a) , *C. liberica* Bull. ex Schum., *C. robusta* L. Linden, *Cola acuminate* Schott and Endl., *Cordia dodecandra* DC., *Crotalaria* L. sp., *C. anagyroides* Kunth, *C. usaramoensis* Baker, *Dalbergia latifolia* Roxb., *Dendrobium* Sw. sp., *D. phalaenopsis* Fitzq., *D. superbum* Rchb., *D. veratrifolium* Lindl., *Derris microphylla* (Miq.) B.D. Jacks, *Didymopanax*

Decne. and Planch. sp., *Dryobalanops oblongifolia* Dyer, *Endospermum malaccense* Muell.-Arg., *Epidendrum stamfordianum* Bateman , *Erythrina lithosperma* Miq. Var, *inermis* Kds. and Val., *Erythroxylon novogranatense* Hieron., *Esenbeckia pentaphylla* Griseb., *Eugenia polyantha* Phil., *Eupatorium pallescens* DC., *Eusideroxylon zwageri* Teijsm. and Binn., *Ficus* L. sp., *Ficus ampelas* Burm., *Fissistigma elegans* Merr., *Flemingia strobilifera* (L.) W.T. Aiton, *Freycinetia hombroni* Martelli, *Fuchsia* L. sp., *Glochidion* J.R. Forst. and G. Forst. sp., *Grewia laevigata* Vahl, *Gynotroches onillaris* Blume, *Hevea brasiliensis* Muell.-Arg., *Intsia palembanica* Miq., "Laurel roja" (Venezuela), *Lecythis* Loefl. sp., *Leucaena glauca* Benth., *Licania hypoleuca* Benth., *Lonicera caprifolium* L., *Macaranga* Thou. sp., *Machaerium cirrhiferum* Pittier, *Marumia muscosa* Blume, *Melia azedarach* L., *Miconia trinervia* Coqn., *Ochroma lagopus* Sw., "Palito negro" (Venezuela), *Persea gratissima* Gaertn., *Phalaenopsis* Blume sp., *Pometia pinnata* Forst., *Pouteria sapota* (Jacq.) H.E. Moore and Stearn, *Quararibea* Aubl. sp., *Renathera storiei* Rchb., *Sambucus javanica* Reinw. ex Blume, *Schizolobium parahyba* (Vell.) Blake, *Schleichera oleosa* Merr., *Serjania* Mill. sp., *Shorea* Roxb. ex C.F. Gaertn sp., *S. leprosula* Mil., *Spondias mombin* L., *Swietenia macrophylla* King, *S. mahagoni* (L.) Jacq., *Tabebuia rosea* DC., *Tarenna incerta* Koord. and Valeton, *Tectona grandis* L., *Tephrosia* Pers. sp., *T. maxima* Pers., *T. vogelii* Hook, *Thea sinensis* L., *Theobroma cacao* L., *Terminalia amazonica* (J.F. Gmel.) Exell, *Trema micrantha* (L.) Blume, *T. orientale* Blume, *Vanda* Jones ex. R.Br. sp., *V. coerulea* Griff. ex Lindl., *V. teres* Lindl., *V. tricolor* Lindl., *Vitis* L. sp.

Specimens examined.— (197 ♀; 13 ♂) Type material: Lectotype *Xyleborus difficilis* (♀; USNM). Allotype *Xylosandrus difficilis*: Java, Bnadya, VII-33, L.G.E. Kalshoven (♂; NHMW). Cotype *Xyleborus difficilis*: Java: Coll. Hagedorn, 1915 (♀; NHMW). Lectotype *Xyleborus luzonicus*: Mt. Makiling, Luzon, Baker, Eggers collection 1948 (♀; USNM). Paratype *Xyleborus abruptoides*: Fiji: Viti Levu, Navai Mill, Nr. Nandarivatu, 2500 ft., 15.IX.1938, beating shrubbery (♀; NHMW).

Other material: **Australian Region:** Australia: In *Phalaenopsis* sp. VI-17-35 (17 ♀, 1 ♂; USNM); Australia, on *Vanda coerulea*, VI-25-1938 (3 ♀; USNM); Australia: In *Vanda coerulea*, VII-7-36 (9 ♀, 3 ♂; USNM); Australia, Fullaway, Nov. 26 1934, *Dendrobium phalaenopsis* (1 ♀; USNM); Australia: Brisbane, S. F., 3/1/49. In Quar., *Dendrobium phalenopsis* host, collector Art Retan (4 ♀, 1 ♂; CAS). Solomon Islands: Solomon Islands: Guadalcanal, Mt. Austin. 11 Jan 1984, M. Bigger, boring in *Pometia pinnata* midrib (1 ♀; BMNH). **Nearctic Region:** United States: New Jersey, Bound Brook, Aug 14/16, B. Weiss Harry colr., *Cattleya* (6 ♀, 3 ♂; USNM). **Neotropical Region:** Colombia: Colombia: 24 km E Barbosa, VII-18-70, Antioquia, el. 1200 m, S.L. Wood, Lauraceae (1 ♀; USNM); Colombia: 24 km E Barbosa, VII-18-70, Antioquia, el. 1200 m, S.L. Wood, *Xylopia* sp. (2 ♀; USNM); Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el. 30 m, S.L. Wood, *Aspidosperma* sp. (5 ♀; USNM); Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el. 30 m, S.L. Wood, *Lecythis* sp. (1 ♀; USNM); Colombia: 8 km S Colonia V. de Cauca, VII-9-70, el. 30 m, S.L. Wood, *Chrysophyllum catmito* (1 ♀; USNM). Costa Rica: Costa Rica: Pandora lim., 150 ft., VIII-23-1963, S.L. Wood, *Cecropia* sp. leaf petioles (1 ♀; USNM); Costa Rica: San Jose, Santa Ana, 4000 ft., X 4–1963, S.L. Wood, unknown limb (1 ♀; USNM). Ecuador: Ecuador: Galap: St. Cruz, 1.7 km N St, Rosa, 1-30.V.91, 550 m, Scalesia, mal-FIT, S. and J. Peck (2 ♀; CAS); Ecuador, Napo Prov., Rees. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39′10″S, 076°26′W, 220 m. elev., July 1995, T. L. Erwin, et al collectors (1 ♀; USNM); Ecuador, Napo Prov., Rees. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39′10″S, 076°26′W, 220 m. elev., January 1996, T. L. Erwin, et al collectors (1 ♀; USNM); Ecuador, Napo Prov., Rees. Ethnica Waorani, 1 km S. Onkone Gare Camp, Trans. Ent. 00°39′10″S, 076°26′W, 220 m. elev., July 1996, T. L. Erwin, et al collectors (3 ♀; USNM); Ecuador, Napo Prov., Tiputini Biodiversity Station, 220-250 m, October 1998, 00°37′55″S, 076°08′39″W, T. L. Erwin, et al collectors (3 ♀; USNM). Honduras: Honduras, at Tampa, 28-III-1968, J. Jordan, in orchid plnt. stem (1 ♀; USNM); Honduras: Zamorano, Moraz, 2200 ft., IV-18-1946, S.L. Wood, *Serjania* (2 ♀; USNM). Mexico: OAX, Romero 18 mi N, 400 ft, VI-29-1967, S.L. Wood, unknown twig (1 ♀; USNM); Mexico: OAX, Romero 18 mi N, 400 ft, VI-29-1967, S.L. Wood, unknown branch (1 ♀; USNM); Mexico: OAX, Romero 23 mi N, VI-29-1967, 300 ft., S.L. Wood, unknown branch (1 ♀; USNM); Mexico: VC, Coatzocoalcos, 18 mi E, VI-26-1967, el. 100ft., S.L. Wood, unknown log

(2 ♀; USNM); Mexico, Vera Cruz, and Oaxaca, 24-VIII-66, Cool. G. Schwenke, Orchids and bromeliads (8 ♀; USNM). Nicaragua: Finca San Pedro, Matagalpa, 10-IV-81, en tallo de Cacao, Coll. J.A. Estrada (4 ♀; USNM). Panama: Ancon, C.I., 18.VII-45, *Epidendrum stamfordianum* Broelle (1 ♀; USNM), Barro Colorado, CZ Panama, 16, 19, 21/5 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 25, 28, 30. IV.1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 22, 24, 26. IX. 1986, Henk Wolda (6 ♀; UCDC); Barro Colorado, CZ Panama, 28, 31/3. 2/4. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 20-24.X.1986, Henk Wolda (4 ♀; UCDC); Barro Colorado, CZ Panama, 25-29.V.1987, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 1-5.VI.1987, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 1-5.XII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 23-27.II.1987, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 15, 17, 19. IX.1986, Henk Wolda (3 ♀; UCDC); Barro Colorado, CZ Panama, 4, 8, 9. IV. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 14, 17, 19, .III. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 9, 12, 14. V. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 1, 3, 5.IX.1986, Henk Wolda (13 ♀; UCDC); Barro Colorado, CZ Panama, 25, 27. VIII. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 18, 21, 23. IV. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 29.IX/1,3.X.1986, Henk Wolda (6 ♀; UCDC); Barro Colorado, CZ Panama, 8-12.XII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 11, 14, 16/4.1986, Henk Wolda (3 ♀; UCDC); Barro Colorado, CZ Panama, 2, 5, 7/5. 1986, Henk Wolda (2 ♀; UCDC); Barro Colorado, CZ Panama, 31-I/3-II.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 6, 9, 11.VI.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 7, 9, 11.VII.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 18, 20, 22.VIII. 1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 13, 15, 17.X.1986, Henk Wolda (1 ♀; UCDC); Barro Colorado, CZ Panama, 21, 23, 25.VII.1986, Henk Wolda (1 ♀; UCDC); Panama: Barro Colo Is. OZ, 1-II-45, J. Zetek (3 ♀; USNM); Barro Colo. Is., CZ, Mar. Apr. 49, Zetek (1 ♀; USNM); Barro Colorado Isl., CZ, XII-46-II-47 J Zetek collector (1 ♀; USNM); Panama: Barro Colorado Island, CZ, VII-23-1966, S.L. Wood, unknown log (1 ♀; USNM); CZ Panama, Lion Hill, VI 21 1982, R.B. Kimsey Col. (1 ♀; UCDC); Panama: CZ, Ft Amador, VII-27-66, S.L. Wood, unknown twigs (4 ♀; USNM); Panama: CZ, Gatun Dam, 40 ft., XII-31-1963, S.L. Wood, *Cecropia* sp. leaf petioles (2 ♀; USNM); Panama: Panama Prov., 6-8 km N El Llano on El Llano-Carti Road, VI-6-1994, F. Andrews and A. Gilbert (1 ♀; CSCA); Panama: Panama Prov. 9 km N El Llano, V-21-1993, F. Andrews and A. Gilbert (1 ♀; CSCA). Venezuela: Venezuela 9 km S of Barrancas, Barinas, 150 m, XI-5-69, S.L. Wood, *Spondias mombin* (2 ♀; USNM); Venezuela: 9 km S of Barrancas, Barinas, 150 m, XI-5-69, S.L. Wood, *Inga* (1 ♀; USNM); Venezuela: 8 km SW Bumbum, Barinas, II-11-1970, 150 m, S.L. Wood, Cucurbitaceae (1 ♀; USNM); Venezuela: 20 km SE El Vigia Merida, XII-10 69, el. 50 m, S.L. Wood, unknown vine (1 ♀; USNM); Venezuela: Finca Monasterios, Cacaugua, Mir., 1971, *Theobroma cacao* (1 ♀; USNM). Sanat Domingo, 25-I-1980, Coffee, J. Esenbar (1 ♀; USNM); Venezuela: 40km SE Socopo, Barinas, I-25-1970, 150 m, S.L. Wood, Palito negro (1 ♀; USNM); Venezuela: 40 km SE Socopo, Barinas, I-25-1970, 150 m, S.L. Wood, Laurel roja (1 ♀; USNM). **Oceania:** Fiji Islands: Fiji, Viti Levu, Nadarivatu, VIII.1955, B.A. O'Connor, young mahogany (2 ♀; NHMW). Samoan Islands: Samoa: Afiamalu, Upolu, VII-10-40, beating dead branches, E. C. Zimmerman collector (1 ♀; NHMW). **Oriental Region:** Indonesia: Java, Bnadya, VII-33, L. G.E. Kalshoven (2 ♀; NHMW). India: Coffee Res Sub-station, Chethalli, Karnataka, Sp. 70. on *Coffea robusta* (1 ♀; BMNH); Java: W Bandjar, 1933, leg. Kalshoven, *Tectona* (2 ♀; USNM). La Reunion, Saint Pierre, 17.X.1989, Orchidee, S. Quilici (3 ♀; USNM). Malaysia: Malaya: Kelantan, I:VII:1947, F.G. Browne (3 ♂; BMNH). Philippine Islands: Philippines, X-23-63, E. Shiroma and E. Davidson, in orchid sp. (1 ♀; USNM); Philippine Is., Apr. 2, 1940, In *Renanthera storiei* (1 ♀; USNM); Philippine Is., *Dendrobium superbum*, E. Arbios, Sept.19.1933 (1 ♀; USNM). Sri Lanka: Ceylon [Sri Lanka]: Peradeniya, 29.VII.1914, A. Rutherford (1 ♀; NHMW); Sri Lanka: Kal. Dist., Morapitiya, 250 mtrs., 27 May 1975, S.L. Wood (1 ♀; USNM). **Palearctic Region:** United Kingdom: England, St. Albans, *Dendrobium phalenopsis*, IV-25-30, E. Rannells, intercepted Washington D.C. (3 ♀, 4 ♂; USNM).

Xylosandrus nanus (Blandford), nomen dubium

Xyleborus nanus Blandford, 1896b:242. Holotype ♀: Noumea (Delauney); Location of holotype unknown.
Xylosandrus nanus (Blandford): Browne, 1963:55.

NOTES.— *Xylosandrus nanus* was described from a single specimen by Blandford in 1896. When Browne (1963) transferred the species to *Xylosandrus*, he noted that it was "probably at most a variation of *X. morigerus*." Furthermore, Wood and Bright (1992) incorrectly cite the holotype as housed in the BMNH. Since Blandford did not indicate where the holotype was deposited in his original description, the location of the holotype is unknown. Therefore, the authors were unable to examine any specimens of *X. nanus*. Blandford distinguished it from *X. morigerus* by the characters of minute granules and setae on the elytral declivity. Among several hundred specimens examined from New Caledonia, not one corresponded to *X. nanus* (Beaver pers. comm). Given that after over 100 years *X. nanus* is still only known from the holotype, the validity of this species is doubtful.

DISTRIBUTION.— **Oceania:** New Caledonia.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— Unable to examine any specimens (see notes above).

Xylosandrus pusillus (Schedl)

Figure 36.

Xyleborus pusillus Schedl, 1961a: 91. Holotype ♀: Luzon, Rizal, Mt. Irid; NHMW.
Xylosandrus pusillus (Schedl): Schedl, 1964:213.

DIAGNOSIS.— Female 1.5–1.7 mm long; 1.9 times longer than wide. Body light brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with a lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibial teeth not visible on specimen examined; metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins carinate to 7th interstriae. Six striae visible on declivity. Striae punctate, with semi-appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

This species is morphologically similar to *X. compactus* (Fig. 14) and *X. curtulus* (Fig. 17). It can be distinguished from *X. curtulus* by a pronotal disc that is evenly pubescent, rather than mostly glabrous. *Xylosandrus pusillus* is nearly morphologically identical to *X. compactus*. The only character distinguishing the two species is the degree of body stoutness, with *X. pusillus* being 1.9 times as long as wide and *X. compactus* being 2.3 times as long as wide. However, this is too large a disparity to warrant synonymizing the two species without further investigation.

DISTRIBUTION.— **Oriental Region:** Philippines (Luzon).

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (1 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xyleborus pusillus* (♀; NHMW).

Xylosandrus pygmaeus (Eggers)

Figure 37.

Xyleborus pygmaeus Eggers, 1940: 142. Holotype ♀: Ost-Java (Alas Tbedek) leg. Bedemann; NHMW.
Xylosandrus pygmaeus (Eggers): Browne, 1963: 55.

Diagnosis.— Female 1.3–1.4 mm long; 2.3 times longer than wide. Body light brown to brown; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum of equal length and width. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate basally. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 6 socketed teeth; metatibiae with 5 socketed teeth. Elytra times 1.2 longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Five striae visible on declivity. Striae punctate, without setae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. borneensis* (Fig. 12). *Xylosandrus pygmaeus* can be distinguished from *X. borneensis* by the following characters: elyral declivity with striae less impressed; five striae visible on declivity; declivital striae with erect or semi-erect, hair-like setae, longer than the width of the second declivital interstriae; and pronotum with a lateral costa, but not carinate.

Distribution.— **Oriental Region:** Indonesia (Java), Malaysia, Sri Lanka.

Hosts.— *Litsea amara* Blume, *Vitex pubescens* Vahl.

Specimens examined.— (11 ♀; 0 ♂) Type material: Holotype *Xyleborus pygmaeus* (1 ♀; NHMW).

Other material: **Oriental Region:** Indonesia: E. Java: Bangelan, 14.5.1932 (1 ♀; USNM); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot B, ca 300 m Lowland Forest, Mar-85, Flight intercept trap (1 ♀; RAB). Malaysia: Brunei: Temburong: Nr. K. Belalong Field, Study Centre 150 m, 4°33'N 115°09'E, 21.ii.1992, R.A. Beaver, RGS/UBD Exped. (1 ♀; RAB); Malaysia: Sabah Sipitang, Mendolong, T6/R, 14.iii.1989, leg. S. Abdebratt (1 ♀; RAB); Malaysia: Sabah Sipitang, Mendolong, T5/R, 10.iii.1989, leg. S. Abdebratt (1 ♀; RAB); Malaysia: Sabah Sipitang, Mendolong, T6/R, 14.iii.1989, leg. S. Abdebratt (1 ♀; RAB); Malaysia: Sabah Sipitang, Mendolong, T6/R, 11.v.1988, leg. S. Abdebratt (1 ♀; RAB); Malaysia: Sabah Sipitang: Mendolong, T5/R, 28.iv.1988, leg. S. Abdebratt, comps. Sp'm det. F. G. Browne (1 ♀; RAB); Selegor, Kejang, 25. 1. 1949, F.G. Browne, ex *Vitex pubescens* (1 ♀; BMNH). Sri Lanka: Ceylon [Sri Lanka]: W. Prov., Labugama, 24 miles ESE Colombo, 21.I.62, in sweep net (1 ♀; NHMW).

Xylosandrus queenslandi Dole and Beaver

Figure 38.

Xylosandrus queenslandi Dole and Beaver, 2008. Holotype ♀: AUSTRALIA, Queensland, Bunya Mountain NP, 1100m, ex Leguminosae tree, 19.i.2000 (B. Jordal and A. Sequeira); QMB.

Diagnosis.— Female 1.6–1.9 mm long; 2.2 times longer than wide. Body light brown to brown; elytra slightly darker than pronotum; antennae and appendages light brown. Frons reticulate and sparsely punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9

times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presense of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin, meso- and metatibiae with 7–9 socketed teeth. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margin marked by a row of coarse, closely placed serrations. Six striae visible on declivity. Striae coarsely granulate, with erect, tapered hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is one of three *Xylosandrus* with lateral declivital margins that are marked by coarse serrations: *X. abruptulus* (Fig. 6), *X. corthyloides* (Fig. 15), and *X. queenslandi*. *Xylosandrus queenslandi* can be distinguished from *X. corthyloides* by the presence of a dense patch of mycangial setae on the basal pronotum. *Xylosandrus queenslandi* can be distinguished from *X. abruptulus* by the following characters: declivital face steep and abruptly separated from disc; declivity matte; and declivital striae with erect, acutely tapering, hair-like setae, shorter than the width of the second declivital interstriae.

DISTRIBUTION.— **Australian Region:** Australia (Queensland).

HOSTS.— *Argyrodendron actinophyllum* (Bailey) Edlin.

SPECIMENS EXAMINED.— (2 ♀; 0 ♂) TYPE MATERIAL: Paratypes *Xylosandrus queenslandi*: Australia: Queensland, Bunya mountains National Park, Jan. 2000, 1100 m, ex. Leguminosae tree, 19.1 B. Jordal and A. Sequeira leg. (2 ♀; MSU).

Xylosandrus rotundicollis (Browne), new combination

Figure 39.

Xyleborus rotundicollis Browne, 1984:73. Holotype ♀: New Guinea: Morobe District, Mount Kaindi, 2350 m, 4.XI.1972; BMNH.

DIAGNOSIS.— Female 2.5–3.2 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae narrowly, but completely separated. Protibiae with 6 socketed teeth on lateral margin; mesotibiae with 9–10 socketed teeth; metatibiae with 9–11 socketed teeth. Elytra 1.4 times longer than wide; 2.1 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins rounded, without a carina or a row of tubercles or serrations. Six striae visible on declivity. Striae punctate, with semi-appresssed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Xylosandrus rotundicollis was recovered as sister species to *X. russulus* in a molecular phylogeny containing many *Xylosandrus* spp. (Dole et al., in review). However, the two taxa are separated by appreciable molecular distance and can be distinguished by several morphological characters.

This species is morphologically similar to *X. monteithi* (Fig. 33) and *X. russulus* (Fig. 40). *Xylosandrus rotundicollis* can be distinguished from *X. monteithi* by the following characters: 2.5 mm long; basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium; declivital striae with semi-appressed, hair-like setae, shorter than the width of the second declivital interstriae; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of the second declivital interstriae. *Xylosandrus rotundicollis* can be distinguished from *X. russulus* by the following characters: 2.5–3.2 mm long; elytral surface shining; prosternal posterocoxal process less pointed; protibiae broadened toward apex, armed with 6 socketed teeth.

DISTRIBUTION.— **Australian Region:** Papua New Guinea.

HOSTS.— *Ficus* L. sp., *F. mollior* Benth., *Gordonia* Ellis sp., *Meliosma* Blume sp., *Schefflera* sp. J. R. Forst and G. Forst.

SPECIMENS EXAMINED.— (5 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xyleborus rotundicollis* (♀; BMNH).

OTHER MATERIAL: **Australian Region:** Papua New Guinea: Papua New Guinea, Mu village, March 2006, 1600 m asl, Hulcr and Cognato coll. (4 ♀; MSU).

Xylosandrus russulus (Schedl), new combination

Figure 40.

Xyleborus russulus Schedl, 1942c:187. Holotype ♀: Neu-Guinea; NHMW.
Euwallacea russulus (Schedl): Wood and Bright, 1992:693.

NOTES.— This species was first included in *Euwallaca* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DIAGNOSIS.— Female 3.5–4.2 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.7 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae narrowly, but completely separated. Protibiae with 7 socketed teeth on lateral margin; mesotibiae with 10 socketed teeth; metatibiae with 11 socketed teeth. Elytra 1.4 times longer than wide; 3.4 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margins rounded, without a carina or a row of tubercles or serrations. Six striae visible on declivity. Striae punctate, with semi-appresssed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, uniseriate, with erect, hair-like setae, longer than twice the width of second declivital interstriae.

Xylosandrus russulus was recovered as sister species to *X. rotundicollis* in a molecular phylogeny containing many *Xylosandrus* spp. (Dole et al., in review). However, the two taxa are are divided by appreciable molecular distance and can be distinguished by several morphological characters.

This species is morphologically similar to *X. monteithi* (Fig. 33) and *X. rotundicollis* (Fig. 39). *Xylosandrus russulus* can be distinguished from *X. monteithi* by the following characters: basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium; declivital striae with semi-appressed, hair-like setae, shorter than the width of the second declivital interstriae; and declivital interstriae uniseriate granulate, with erect, hair-like setae, longer than twice the width of the second declivital interstriae. *Xylosandrus russulus* can be distinguished from *X. rotundicollis* by the following characters: 3.5–4.2 mm long; elytral surface not duller, lacking opalescence; prosternal posterocoxal taller, pointed; protibiae narrow toward apex, armed with 7 socketed teeth.

DISTRIBUTION.— **Australian Region**: Papua New Guinea.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (52 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xyleborus russulus*: Papua New Guinea (NHMW).

OTHER MATERIAL: **Australian Region:**Papua New Guinea, Kupa Range, Morobe, 2000 m., glue trap, Roberts coll. (1 ♀; FICB). Papua New Guinea: Chimbu Prov, J. Hulcr 2002-2006 (50 ♀; MSU).

Xylosandrus subsimiliformis (Eggers)

Figure 41.

Xyleborus subsimiliformis Eggers, 1939a:11. Holotype ♀: Nordostbirma (Kaim, 7000 Fuss) 17.V.1934; NHR (Eggers Paratype in NHMW).

Xylosandrus subsimiliformis (Eggers): Wood and Bright, 1992:800.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination."

DIAGNOSIS.— Female 2.8 mm long; 2.1 times longer than wide. Body brown; antennae and legs same color as body. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture or semi-appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; mesotibiae with 10 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.2 times longer than wide; 1.3 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae granulate, with appressed, hair-like setae, shorter than the width of second declivital interstriae. Interstriae finely granulate, multiseriate, with appressed, hair-like setae, shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beesoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 20), and *X. jaintianus* (Fig.27). *X. subsimiliformis* can be distinguished from these species by the following characters: declivity flattened; pronotum with a conspicuous summit on basal third; four striae visible on elytral declivity; and frons punctate, without a distinct median keel.

DISTRIBUTION.— **Oriental Region:** Burma, Thailand.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (4 ♀; 1 ♂) TYPE MATERIAL: Paratype *Xyleborus subsimiliformis*: N.E. Burma, Kambaiti, 7000 ft., 12.5.1924, R. Malaise (♀; NHMW).

OTHER MATERIAL: **Oriental Region:** Thailand: Chiang Mai: Doi Pui, 16.I.05, R. A. Beaver (1 ♀; RAB); Thailand: Chiang Mai, Doi Suthep, c.1400m, 18.x.04, R. A. Beaver (2 ♀, 1 ♂; RAB).

Xylosandrus subsimilis **(Eggers)**

Figure 42.

Xyleborus subsimilis Eggers, 1930:186. Holotype ♀: Assam (Shillong, 6000 ft); FRI.
Xylosandrus subsimilis (Eggers): Wood and Bright, 1992:800.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors failed to indicate it as a "new combination."

DIAGNOSIS.— Female 2.6 mm long; 2.0 times longer than wide. Body brown; antennae and legs same color as body. Frons rugose. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.9 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi- appressed, hair-like setae; setae less dense on disc. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pronotal-mesonotal mycangium. Pronotal disc densely asperate-granulate, with sculpture separated by distance less than or equal to their width. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4–5 socketed teeth on lateral margin; mesotibiae with 9–11 socketed teeth; metatibiae with 10 socketed teeth. Elytra 1.1 times longer than wide; 1.2 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Declivital face steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Four striae visible on declivity. Striae coarsely granulate, with appressed, scale-like setae, shorter than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed, scale-like setae shorter than the width of second declivital interstriae.

This species is morphologically similar to *X. beesoni* (Illustrated in Saha et al. 1992), *X. discolor* (Fig. 20), *X. jaintianus* (Fig. 27), and *X. subsimiliformis* (Fig. 41). However, *X. subsimilis* can easily be distinguished from these species by its declivital vestiture of dense, flattened, scale-like setae.

DISTRIBUTION.— **Oriental Region:** China, India (Assam, Bengal), Thailand.

HOSTS.— *Cinnamomum obtusifolium* Nees., *Tectona grandis* L., *Terminalia myriocarpa* Van Heurck and Müll. Arq.

SPECIMENS EXAMINED.— (5 ♀; 0 ♂) TYPE MATERIAL: Paratype *Xyleborus subsimilis*: Shillong, 6000 ft, C. F. C. Beeson, 14.V.1925, ex. unknown wood (1 ♀; NHMW).

OTHER MATERIAL: **Oriental Region:** China: China, 1962.VII (2 ♀; USNM). India: Samsingh 1800, Kalimpong, Bengal, 4.X.33, C. F. C. Beeson. ex. *Cinnamomum obtusifolium* branches (2 ♀; USNM).

Xylosandrus terminatus **(Eggers)**

Figure 43.

Xyleborus terminatus Eggers, 1930:182. Holotype ♀: Coorg (Virojapet, Sidapur); FRI.
Xylosandrus terminatus (Eggers): Browne, 1963:55.

DIAGNOSIS.— Female 1.5–1.9 mm long; 2.1 times longer than wide. Body dark brown to black; antennae and legs yellowish brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed, hair-like setae; pronotal disc glabrous, except for mycangial setae. Basal pronotum with a dense patch of short, erect setae, indicating the presence of a pornotal-mesonotal mycangium. Pronotal disc moderately punctate. Lateral aspect of pronotum basic (type 0, Hulcr et al. 2007). Pronotum with lateral costa and carina. Procoxae widely separated. Protibiae with 4 socketed teeth on lateral margin; meso- and metatibial teeth not visible on specimens examined. Elytra 1.2 times longer than wide; 1.4 times longer than pronotum. Discal striae punctate; interstriae uniseriate punctate. Declivital face of elytra steep and abruptly separated from disc. Declivity flattened, lateral margins carinate to 7th interstriae. Striae punctate, without setae. Interstriae punctate, uniseriate, with erect, hair-like setae, longer than the width of second declivital interstriae.

This species is morphologically similar to *X. derupteterminatus* (Fig. 18) and *X. morigerus* (Fig. 35). *Xylosandrus terminatus* can be distinguished from *X. morigerus* by the following characters: elytral declivity flattened; and five striae visible on declivity. *Xylosandrus terminatus* can be distinguished from *X. derupteterminatus* by the following characters: smaller species, 1.5–1.9 mm long; interstrial setae longer than the width of second declivital interstriae; and declivital interstriae uniseriate punctate.

DISTRIBUTION.— Oriental Region: India (Karnataka, Maharashtra, Tamil Nadu).

HOSTS.— *Holigarna arnottiana* Hook, *Lantana* L. sp., *Swietenia macrophylla* King.

SPECIMENS EXAMINED.— (3 ♀; 0 ♂) TYPE MATERIAL: Paratype *Xyleborus terminatis*: Coorg, Virojapet, Sidapur, Y. R. Rao coll., 9. XI.1917, boring into twigs of Lantana (♀; NHMW).

OTHER MATERIAL: **Oriental Region:** India: Chandanthode, Wynadd, Madras. Research Forester., 8.XII.1938, ex *Swietenia macrophylla* stump (2 ♀; USNM).

Xylosandrus woodi Dole and Beaver

Figure 44.

Xylosandrus woodi Dole and Beaver, 2008. Holotype ♀: [Australia], NEQ[ueensland], 16°30'S x 145°19'E, Mt Demi summit, 1100 m, flight intercept, 17.xii.1995-22.i.1996 (Monteith, Thompson and Ford). In QMB (Accession # T144404).

DIAGNOSIS.— Female 2.3–2.4 mm long; 2.1 times longer than wide. Body dark brown; antennae and legs light brown. Frons punctate. Antennae with 5 funicular segments. Antennal club obliquely truncate; first segment forming a circular costa; segment one covering entire posterior face. Pronotum 0.8 times longer than wide. Dorsal aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotal vestiture of semi-appressed hair-like setae; pronotal disc densely setose, with setae as dense as on anterior pronotum. Lacking a dense patch of setae at base of pronotum. Pronotal disc densely asperate-granulate. Lateral aspect of pronotum rounded (type 1, Hulcr et al. 2007). Pronotum with lateral costa, not carinate. Procoxae widely separated. Protibiae with 4–5 socketed teeth on lateral margin; meso- and metatibiae with 7-8 socketed teeth. Elytra 1.3 times longer than wide; 1.6 times longer than pronotum. Discal striae punctate; interstriae multiseriate punctate. Elytral disc gradually curving into declivity. Declivity convex, lateral margin with discontinuous row of small tubercles, some of these towards apex with carinate tip. Five striae visible on declivity. Striae punctate, with appressed, hair-like setae, longer than the width of second declivital interstriae. Interstriae granulate, multiseriate, with appressed hair-like setae, longer than the width of second declivital interstriae.

This species can be distinguished from all other known *Xylosandrus* by its lateral declivital margin which is marked by a discontinuous row of small tubercles. *Xylosandrus woodi* may be confused with *X. monteithi* (Fig. 33) and *X. rotundicollis* (Fig. 39), but these two species have lateral declivital margins that are rounded and without a row of tubercles.

DISTRIBUTION.— Australian Region: Australia (Queensland).

HOSTS.— Unknown.

Specimens examined.— (1 ♀; 0 ♂) Type material: Paratype *Xylosandrus woodi*: Australia: NEQ, 19°07'S, 146°23'E, Mt Halifax summit, 1050m, heath, rainforest, pitfalls, 19-21.iii.1991, G. Monteith and D. Cook (1 ♀; MSU).

New Combinations, *Amasa*

Amasa cylindrotomicus (Schedl), new combination

Pseudoxyleborus cylindrotomicus Schedl, 1939:40. Lectotype ♀: Sumatra, Benkoelen, 23-6-31, leg. Shuller; NHMW; designated by Schedl, 1979a:74.

Xylosandrus cylindrotomicus (Schedl): Wood and Bright, 1992:793.

Xyleborus semitruncatus Schedl, 1942b:35. Lectotype ♂: Sumatra, Manna, 15-IX-34: NHMW; designated by Schedl, 1979a:224. Synonymy: Wood, 1989:177.

Xyleborus truncatellus Schedl, 1951:79. Lectotype ♀: Z. Sumatra, Poelau Pisang, and Manna; NHMW; designated by Schedl 1979a:256. Synonymy: Kalshoven, 1959:95.

Xyleborus jucundus Schedl, 1954:138. Lectotype ♀: Z. Sumatra, Poelau Pisang, and Manna; NHMW; designated by Schedl, 1979a:256. Synonymy: Kalshoven, 1959:95.

Xyleborus ramulorum Schedl, 1957:115. Holotype ♀: Congo Belge: Yangambi; MRCB. Synonymy: Wood, 1989:177.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Afrotropical Region:** Zaire. **Oriental Region:** Indonesia (Sumatra).

Specimens examined.— (4 ♀; 1 ♂) Type material: Lectotype *Pseudoxyleborus cylindrotomicus* (♀; NHMW). Lectotype *Xyleborus semitruncatus* (♂; NHMW). Lectotype *Xyleborus truncatellus* (♀; NHMW). Allotype *Xyleborus truncatellus*: Sumatra, Manna, 25-IX-1934 (♂; NHMW).

Other material: **Oriental Region:** Indonesia: Sumatra, Benkoelen, 23-6-31, leg. Shuller (1 ♀; NHMW).

Discussion.— Based on the contiguous procoxae, antennal club with three segments visible on the anterior and posterior face, elytral declivital face that is steep and abruptly separated from the disc and the circular costa forming a complete circumdeclivital ring, this species is here transferred to *Amasa*.

Amasa omissus (Schedl), new combination

Xyleborus omissus Schedl, 1961b: 153. Holotype ♀: Madagascar, Antaniditra pres Perinet, 18 November 1952, K.E. Schedl; IRSM.

Xylosandrus omissus (Schedl): Wood and Bright, 1992: 799.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Afrotropical Region:** Madagascar.

Specimens examined.— (2 ♀; 0 ♂) Type material: Paratypes *Xyleborus omissus*: Madagascar, Perinet, 17.XI.1952, K. E. Schedl (2 ♀; NHMW)

Discussion.— Based on the contiguous procoxae, antennal club with three segments visible on the anterior and posterior face, elytral declivital face that is steep and abruptly separated from the disc and the circular costa forming a complete circumdeclivital ring, this species is here transferred to *Amasa*.

Amasa oralis (Schedl), new combination

Xyleborus oralis Schedl, 1961b:154. Holotype ♀: Madagascar, Antaniditra pres Perinet, 18 November 1952, K. E. Schedl; IRSM.
Xylosandrus oralis (Schedl): Wood and Bright, 1992:799.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DISTRIBUTION.— **Afrotropical Region:** Madagascar.

SPECIMENS EXAMINED.— (1 ♀; 0 ♂) TYPE MATERIAL: Paratype *Xyleborus oralis*: Madagascar, Perinet, 17.XI.1952, K. E. Schedl (♀; NHMW).

DISCUSSION.— Based on the contiguous procoxae, antennal club with three segments visible on the anterior and posterior face, and elytral declivital face that is steep and abruptly separated from the disc, this species is here transferred to *Amasa*.

New Combinations, *Anisandrus*

Anisandrus butamali (Beeson), new combination

Xyleborus butamali Beeson, 1930:40. Syntypes ♀: Bombay: Agsur, South Kanara, and Dandeli, North Kanara, B. M. Bhatia, Nov.; FRI.
Xylosandrus butamali (Beeson): Wood and Bright, 1992:788.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DISTRIBUTION.— **Oriental Region:** India (Maharaashtra, Tamil Nadu).

SPECIMENS EXAMINED.— (7 ♀; 0 ♂) TYPE MATERIAL: Paratypes *Xyleborus butamali*: Bombay, Agsur, S. Kanara Div., 13.XI.29, B.M. Bhatia, ex. *Dillenia pentagyna* (2 ♀; NHMW).

OTHER MATERIAL: **Oriental Region:** India: S. India: Anamalis Hills, Cinohona, 3500 ft, April 1956, P.S. Nathan (1 ♀; USNM); Kattiyur, Wynaad, Madras, F.R.J. Project, 25.12.1945 (3 ♀; USNM); Manantoddy, N. Malabar, G. C. Robinson, 8.XI.1930, ex *Tectona grandis* (1 ♀; USNM).

DISCUSSION.— Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, protibiae with six socketed teeth, and rounded lateral pronotal margins, this species is here transferred to *Anisandrus*.

Anisandrus ursa (Eggers), new combination

Xyleborus ursa Eggers, 1923:172. Lectotype ♀: Haveri, N. Guinea, S. E., Havari, Loria, VII-XI-93; USNM; designated by Anderson and Anderson, 1971:35.
Xylosandrus ursa (Eggers): Wood and Bright, 1992:801.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DISTRIBUTION.— **Australian Region:** New Guinea, Solomon Islands.**Oriental Region:** Malaysia, Indonesia (Celebes, Sumatra), Philippines (Luzon).

SPECIMENS EXAMINED.— (8 ♀; 0 ♂) TYPE MATERIAL: Lectotype *Xyleborus ursa* (♀; USNM).

OTHER MATERIAL: **Oriental Region:** Indonesia: Indonesia. *Irian Jaya:* PT., Freeport Concession Wapoga, camp. 03.14°S 136.57°E, 3600 ft., 19-29 April 1998, R. R. Snelling, Malaise trap montane primary rainforest (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., 1008 m G. mogongonipa summit, Aug-85, Malaise Trap (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P.G.Mogogonipa summit, 1008 m., Sep-85, Pitfall trap (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P.G.Mogogonipa summit, 1008 m., May-85, Malaise Trap (2 ♀; RAB). Philippine Islands: Luzon, P. I. Baguio Mt. Sto, Tomas W. Schultze (2 ♀; NHMW).

Discussion.— Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, protibiae with seven socketed teeth, and rounded lateral pronotal margins, this species is here transferred to *Anisandrus*.

Anisandrus ursinus **(Hagedorn), new combination**

Xyleborus ursinus Hagedorn, 1908:381. Holotype ♀: Sumatra, Si-Rambe; MNB.
Xylosandrus ursinus (Hagedorn): Wood and Bright, 1992:801.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oriental Region:** Indonesia (Borneo, Soemba Island, Sumatra), Philippines (Mindoro).

Specimens examined.— (9 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** Indonesia: Dammerman, N.O. Soemba, Kambera, III.1925 (1 ♀; NHMW); Sumatra: Solok, Coll. F. Schneider, 1911 (1 ♀; MTD). Philippine Islands: Philippine Islands: Glog Riv., Mt. Apo, Mindanao, IX.29,30, Altitude 6000 ft., Coll. by C.F. Clagg (2 ♀; FMNH); Philippine Islands: La Lun Mts. Davao Prov., Mindanao, I.1.31, Coll. by C.F. Clagg, at light (1 ♀; FMNH); Mindoro, Port Galera, Mc Gregor (2 ♀; USNM); Mt. Makiling, Laguna P. I., 7-21-22, F. C. Hagedorn Collection (1 ♀; USNM); Philippine Islands: Seliban Riv., Mt. Apo, Mindanao, VII.30.30, Altitude 6000 ft., Coll. by C.F. Clagg (1 ♀; FMNH).

Discussion.— Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, protibiae with seven socketed teeth, and rounded lateral pronotal margins, this species is here transferred to *Anisandrus*.

Anisandrus ursulus **(Eggers), new combination**

Xyleborus ursulus Eggers, 1923:173. Holotype ♀: Ost Bali, Kintamani, E. Sundainseln, 1913; MTD.
Xylosandrus ursulus (Eggers): Wood and Bright, 1992:801.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oriental Region:** China (Fujian), India (Bengal, Nicobar Islands), Malaysia, Thailand, Indonesia (Bali, Borneo, Java, Sumatra), Philippines (Luzon).

Specimens examined.— (29 ♀; 1 ♂) Type material: Holotype *Xyleborus ursulus* (♀; MTD). Cotype *Xyleborus ursulus*: Java: Batoerranden, G. Slamet, F.C. Drescher, 19.VII.1930 (♂; NHMW).

Other material: **Oriental Region:** India: Samasingh, Kalimpong, Bengal, III.1934, Mohal Lall. (3 ♀; USNM); Kamsingh, 1800, Kalimpong, Bengal, 22.III.34, C.F.C. Beeson, ex *Sterculia colorata* or *Sapium eugeniaefolium* (2 ♀; USNM). Indonesia: Java: Batoerraden, G. Slamet, F. C. Drescher, 22.III.1930 (5 ♀; USNM); Java: Batoerranden, G. Slamet, F.C. Drescher, 10.IV.1930 (2 ♀; NHMW); Java: Mount Gede, 1900 m, XI-1932, L.G.E. Kalshoven (1 ♀; USNM); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot B, ca 300 m Lowland Forest, Apr-85. Flight intercept trap (2 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., G.Mogogonipa summit, 1008 m, May-85, Malaise Trap (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Oct-85 (1 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, Apr-85, Flight intercept trap (2 ♀; RAB); Indonesia: Sulawesi Utara, Dumoga-Bone N.P., Plot C, ca 400 m lowland forest, May-85, Flight intercept trap (1 ♀; RAB). Malaysia: Malaya: Pahang: Pulau Tioman:

Kampong Tekek, to Kampong Juara, 20.iii.1962, K. J. Kuncheria Collector Bishop, In Jungle (1 ♀; RAB); Malay Penin: Pahang. F.M.S., Faser's Hill, 4200 ft, 28-6-1931 (1 ♀; NHMW); Malaysia: Penang, Penang Hill. 1701, 10.viii.77, R.A. Beaver, Ex. Pitfall trap (1 ♀; RAB); SABAH: Poring Spring, Xanthophyllum affine, Lower montane, 650 m, Mixed dipterocarp Fst., 20. Vi. 1992, A. Floren, Fog Za4/F1 (1 ♀; RAB). Thailand: Thailand: Chiang Mai, Doi Chiang Dao, 12-13.vii.02, A. Cognato, ex ETOH trap on dead tree (1 ♀; RAB); Thailand: Kanchanaburi, 14.70N 98.87E, 17.vii.02, A. Cognato (3 ♀; RAB).

Discussion.— Based on the contiguous procoxae, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, protibiae with seven socketed teeth, and rounded lateral pronotal margins, this species is here transferred to *Anisandrus*.

New Combinations, *Cnestus*

Cnestus ater (Eggers), new combination

Xyleborus ater Eggers, 1923:210. Holotype ♀: Batoe Insel (Tanah Masa); ZMAN.
Xylosandrus ater (Eggers): Wood and Bright, 1992:787.
Xyleborus retusiformis Schedl, 1936:31. Holotype ♀: Borneo; NHMW. Synonymy: Wood, 1989:177.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oriental Region:** China (Fujian), Malaysia, Indonesia (Batoe Island, Borneo).

Specimens examined.— (6 ♀; 0 ♂) Type material: Holotype *Xyleborus retusiformis* (♀; NHMW).

Other material: **Oriental Region:** Brunei: Brunei: Temburong: Nr. K. Belalong Field, Study Centre 300m, 4°33′N 115°09′E, 10.ii.1992, R.A. Beaver, RGS/UBD Exped. Ex. Rattan Calamus Daeninorops (2 ♀; RAB); Brunei: Temburong: Nr. K. Belalong Field, Study Centre 300m, 4°33′N 115°09′E, 10.ii.1992, R.A. Beaver, RGS/UBD Exped. Ex. Calamus Daeninorops sp. (2 ♀; RAB). Indonesia: Padang, ex. Ljengkeh [?], 14.Xii.35, Kalshoven (1 ♀; NHMW).

Discussion.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with six socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus fijianus (Schedl), new combination

Xyleborus fijianus Schedl, 1938:50. Lectotype ♀: Fiji Islands, Taveuni Quilai, 800 feet, October 18, 1924, H.S. Evans; NHMW.
Xylosandrus fijianus (Schedl): Wood and Bright, 1992:794-795.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oceania:** Fiji Islands.

Specimens examined.— (9 ♀; 2 ♂) Type material: Lectotype *Xyleborus fijianus* (♀; NHMW).

Other material: **Oceania:** Fiji: Fiji, Lami Quarry, Nr. Suva, VII-24-38, E.C. Zimmerman collector, beating shrubs, 10′, 250′ (1 ♀; NHMW)I Fiji. Viti Levu, Suva, 22.xi.88, R. A. Beaver, ex *Swietenia macrophylla* (1 ♀; RAB); FIJI, Viti Levu, Savura Creek, 29.iii.83, R.A. Beaver, ex *Serianthea melanesica* (1 ♀; RAB); Fiji, Viti Levu, Namosi 10km, 19-20. V. 85, R.A. Beaver (2 ♀; RAB); FIJI, Viti Levu, Savura Creek, 19.iii.83, R.A. Beaver, ex *Canarium vitiense* (2 ♀; RAB)I; Fiji, Viti Levu, Savura Creek, v.83, R.A. Beaver, ex *Canarium vitiense* (1 ♂; RAB); Fiji, Suva, ex. *Swietenia macrophylla* (1 ♂; BMNH). Fiji, Colo-I-Suva, Static Trap 71, Mahogany plantation, Cpt 23, 10/10/2006, K. Wotherspoon.

Discussion.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with seven socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus gravidus (Blandford), new combination

Xyleborus gravidus Blandford, 1898:427. Holotype ♀: Chittagong Hills [Bangladesh]; BMNH.
Xylosandrus gravidus (Blandford): Wood and Bright, 1992:796.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oriental Region:** Bangladesh, Burma, India (Assam, Bengal), Laos, Sri Lanka, Thailand, Vietnam. **Palearctic Region:** China (Xizang [Tibet]).

Specimens examined.— (2 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** Vietnam: Nord Vietman, L. Thainguyen, VII.1969, leg. Le. Van. Nong (1 ♀; NHMW); Phovi, S 07 (1 ♀; NHMW).

Discussion.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most of the posterior face, the presence of a coarse median pair of asperities on the anterior margin of the pronotum, the protibiae with seven socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus improcerus (Sampson), new combination

Xyleborus improcerus Sampson, 1921:33. Holotype ♀: Siam; BMNH.
Xylosandrus improcerus (Sampson): Beaver, 1998:183.

Distribution.— **Oriental Region:** Brunei, India, Indonesia (Borneo), Malaysia, Thailand.

Specimens examined.— (7 ♀; 0 ♂) Type material: Unable to examine type material.

Other material: **Oriental Region:** Brunei. Brunei: Temburong: Nr. K. Belalong Field, Study Centre 250 m, 4°33'N 115°09'E, 7.ii.1992, R.A. Beaver, RGS/UBD Exped. (3 ♀; RAB); Brunei: Temburong: Nr. K. Belalong Field, Study Centre 250 m, 4°33'N 115°09'E, 21.ii.1992, R.A. Beaver, RGS/UBD Exped. (1 ♀; RAB); Lagleari [?] BC. Sarak, 20:X:1948, F. G. Browne (1 ♀; USNM); Malaysia, Kelantan, E.G.B., 6.10.1946 (1 ♀; USNM); Malaya, Terengganu, Besut Dist., V-1958, R. Traub, 400 ft. (1 ♀; USNM).

Discussion.— Based on the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with six socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus laticeps (Wood), new combination

Xyleborus laticeps Wood, 1977:219. Holotype ♀: 20 km SW El Vigia, Merida, Venezuela; USNM.
Xylosandrus laticeps (Wood): Wood and Bright, 1992:796.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Neotropical Region:** Venezuela.

SPECIMENS EXAMINED.— (51 ♀; 12 ♂) TYPE MATERIAL: *Xyleborus laticeps* (♀; USNM).

OTHER MATERIAL: **Neotropical Region:** Venezuela: Venezuela: 9 km S Barrancas, 150 m, X-1-69, S.L. Wood, *Protium tenuifolium* (13 ♀; USNM); Venezuela: 9 km S of Barrancas, Barinas, 150 m, X-5-69, S.L. Wood (2 ♀; USNM); Venezuela: 9 km S. of Barrancas, Barinas, 150 m, XI-5-69, S.L. Wood, *Spondias mombin* (5 ♀; USNM); Venezuela: 9 km S. of Barrancas, Barinas, 150 m, XI-5-69, S.L. Wood, *Dendropanax arboreum* (1 ♀; USNM); Venezuela: 9 km S Barrancas, Barinas, XII-2-69, el. 150 m, S.L. Wood, *Melicoccous bijugata* (1 ♀; USNM); Venezuela: 8 km SW Bumbum, Barinas, II-11-1970, 150 m, S.L. Wood, *Tartaguito* sp. (2 ♀; USNM); Venezuela: 40 km, E Canton, Barinas, III-8-1970, 70 m, S.L. Wood, *Protium tenuifolium* (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70 m, S.L. Wood, *Palito negro* (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70 m, S.L. Wood, tree seedling (1 ♀; USNM); Venezuela: 40 km E Canton, Barinas, III-8-1970, 70 m, S.L. Wood, *Pouteria anibaefolia* (1 ♀; USNM); Venezuela: 5 km W El Pino, 10 m, Zulia, X-20-69, S.L. Wood, unknown tree (2 ♀; USNM); Venezuela: 20 km SW El Vigio, Merida, XI-21-69, el. 50 m, S.L. Wood, *Jacaranda* sp. (10 ♀; USNM); Venezuela: Merida, 1700 m, IX-22-69, S.L. Wood (4 ♀, 12 ♂; USNM); Venezuela: 40 km SE Socopo, Barinas, I-25-1970, 150 m, S.L. Wood, *Protium* sp. (1 ♀; USNM); Venezuela: 17 km SE of Miri, Barinas, XII-17-69, 150 m, S.L. Wood, *Protium* sp. (1 ♀; USNM); Venezuela: 10 km SE of Miri, Barinas, II-8-1970, 150 m, S.L. Wood, *Inga* sp. (1 ♀; USNM); Venezuela: 7 km NW Socopo, Barinas, II-13-1970, 200 m, S.L. Wood, *Protium* sp. (1 ♀; USNM); Venezuela: Valle de Choroni, IV-3-1964, J.L. Saunders, *Theobroma cacao* (3 ♀; USNM).

DISCUSSION.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with six socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus mutilatus (Blandford), new combination

Xyleborus mutilatus Blandford, 1894c:103. Holotype ♀: Japan; BMNH.

Xylosandrus mutilatus (Blandford): Wood and Bright, 1992:799.

Xyleborus sampsoni Eggers, 1930:184. Holotype ♀: Assam (Haflong, Cachar); FRI. Synonymy: Wood, 1989:177.

Xyleborus banjoewangi Schedl, 1939:41. Lectotype ♀: Banjoewangi, 270 m, Tjoerahlele, 25-II-36; NHMW. Synonymy: Kalshoven, 1960:63.

Xyleborus taitonus Eggers 1939b:118. Holotype ♀: Formosa, Taito; Chujo Collection. Synonmy: Wood and Bright, 1992:799.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer. *Xyleborus taitonus* was also listed as a synonym by Wood and Bright (1992), but was not indicated as a "new synonymy." Wood and Bright (1992) indicate that "Specimens in the FRI, Dehra Dun labeled by Eggers as *taitonus* are *mutilatus*; synonymy needs confirmation", but we were unable to examine the specimens referred to.

DISTRIBUTION.— **Australian Region:** New Guinea. **Nearctic Region:** United States (Florida, Mississippi, Texas). **Oriental Region:** Burma, China (Anhui, Sichuan, Yunnan, Zhejiang), India (Andaman Islands, Assam), Indonesia (Batoe Island, Borneo, Java, Sumatra), Japan, Malaysia, Sri Lanka, Taiwan, Thailand. **Palearctic Region:** Korea.

SPECIMENS EXAMINED.— (34 ♀; 3 ♂) TYPE MATERIAL: Paratype *Xyleborus mutilatus*: Malaya, Selangor, 16:XI:1948, F.G. Browne ex wood of Adenanthera tauonina (♂; BMNH). Lectotype *Xyleborus banjoewangi* (♀; NHMW). Allotype *Xyleborus banjoewangi*: Banjoewangi, II-1936, leg. Baschwesen [?] (1 ♂; NHMW).

OTHER MATERIAL: **Oriental Region:** Japan: JAPAN: Okinawa I., Mt. Oppadake, 20.vi.95, H. Goto, ex

Rhus succedanea (2 ♀, 1 ♂; RAB); Japan: Ryukyus, Mt. Oppadake, Okinawa Is., emerged from the logs, 19.vii.1995, H. Goto leg., Host tree: *Rhus succedanea* L. (1 ♀, 1 ♂; RAB). **Nearctic Region:** United States: Mississippi, Oktibbeha Co., 3 mi W. of Adaton, 33°29′00″N 88°58′13″W, 23-26 April 2004, T.L. Schiefer coll (39 ♀; MSU); Miss., Oktibbeha Co., 3 mi W. of Adaton, 33°29′00″N 88°58′13″W, 17-19 April 2002, T.L. Schiefer, in Lindgren funnel trap (1 ♀; MSU).

DISCUSSION.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with seven socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus orbiculatus (Schedl), new combination

Xyleborus orbiculatus Schedl, 1942a:186. Holotype ♀: Borneo; NHMW.
Xylosandrus orbiculatus (Schedl): Wood and Bright, 1992:800.

NOTES.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

DISTRIBUTION.— **Oriental Region:** Indonesia (Borneo).

SPECIMENS EXAMINED.— (2 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xyleborus orbiculatus* (♀; NHMW).

OTHER MATERIAL: **Oriental Region:** Borneo: British N. Borneo, Tenompok, 15.II.1959, T. C. Maa Collector (1 ♀; RAB).

DISCUSSION.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus peruanus (Wood), new combination

Xylosandrus peruanus Wood, 2007:468. Holotype ♀: Satipo [Junin], Peru, V-VI.1942, Paprzycki; USNM.

DISTRIBUTION.— **Neotropical Region:** Peru (Junin).

SPECIMENS EXAMINED.— (1 ♀; 0 ♂) TYPE MATERIAL: Holotype *Xylosandrus peruanus* (♀; USNM).

DISCUSSION.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the protibiae with six socketed teeth, this species is here transferred to *Cnestus*.

Cnestus retifer (Wood), new combination

Xylosandrus retifer Wood, 2007:468. Holotype ♀: Fazende Laminit, Intinga do Maranhio, Brazil; MZUSP.

DISTRIBUTION.— **Neotropical Region:** Brazil.

SPECIMENS EXAMINED.— (1 ♀; 0 ♂) TYPE MATERIAL: Paratype *Xylosandrus retifer* BR-MA-Itinga do Maranhao, Fazenda Laminit, 6-yr old *Schizolobium nicum* stand, ethanol baited FIT, Ataide, J.A. col. VII/2002 (♀; USNM).

DISCUSSION.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus retusus (Eichhoff), new combination

Xyleborus retusus Eichhoff, 1868:151. Syntypes ♀: N. Freiburg [Brazil]; Hamburg Museum, lost.
Xylosandrus retusus (Eichhoff): Wood and Bright, 1992:800.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Neotropical Region:** Argentina, Brazil.

Specimens examined.— (120 ♀; 0 ♂) Type material: Unable to examine type specimens.

Other material: **Neotropical Region:** Brazil: Nova Teutonia, Sta. Cat., X-56, Plaumann (19 ♀; USNM); Brazil: Nova Teutonia, 27°11′8″S 52°23′1″W, F. Plaumann, 300-500 m, XI.1956 (1 ♀; USNM); Brazil: Nova Teutonia, 27°11′8″S 52°23′1″W, F. Plaumann, 300-500 m, I-1.1957 (1 ♀; USNM); Brazil: Nova Teutonia, 1944, F. Plaumann coll. (5 ♀; USNM); Brasil, Nova Teutonia, Santa Catarina, IX-18-1944, 27°11′S, 52°23′W, Fritz Plaumann collector (1 ♀; AMNH); Brazilen: Nova Teutonia, 28 Oct 1951, F. Plaumann coll. (10 ♀; FMNH); Brazilen: Nova Teutonia, 25 Oct 1951, F. Plaumann coll. (7 ♀; FMNH); Brazilien, Nova Teutonia, 27°11′S 52°23′W, 500m, XI.1947, Fritz Plaumann (8 ♀; FMNH); Brazil, Nova Teutonia, Sta. Catharina, VII.14.1944 (1 ♀; FMNH); Brasilien: Nova Teutonia, 1944, F. Plaumann coll. (3 ♀; NHMW); Brasil, Rio Claro-S. Paulo, Mat no. 5, III-947 [?] (1 ♀; USNM)l Brasil, Rio Claro-S. Paulo, Mat no. 2 III-946[?] (1 ♀; USNM); Brazil: Santa Catharina, Nova Teutonia, 300-500 m, 27°11′S 52°23′W, XI-1947, leg. F. Plaumann (60 ♀; FMNH); Brasil, Varginha, M Gerais, M. Alvarenga leg., III.1972 (1 ♀; NHMW); RS/RGS Exp. Brazil, 12°49′S 51°46′W, 29.xi.1968, R. A. Beaver (1 ♀; RAB).

Discussion.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering the entire posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with six socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

Cnestus testudo (Eggers), new combination

Xyleborus testudo Eggers, 1939b:116. Lectotype ♀: Formosa, Taichu, XI.1930., col. T. Mitono; USNM; designated by Anderson and Anderson, 1971:34.
Xylosandrus testudo (Eggers): Wood and Bright, 1992: 801.

Notes.— This species was first included in *Xylosandrus* by Wood and Bright (1992), but the authors did not indicate it as a "new combination" or cite any characters justifying its transfer.

Distribution.— **Oriental Region:** Taiwan, Thailand, Vietnam.

Specimens examined.— (3 ♀; 0 ♂) Type material: Lectotype *Xyleborus testudo* (♀; USNM).

Other material: **Oriental Region:** Thailand: Thailand: Chiang Mai 600 m, Fang., 17.iii.74, R.A. Beaver, comp. Paralectotypes ex. TARI. (1 ♀; RAB). Vietnam: Tonkin, Reg De Moa binn, A. De Looman, 1929 (1♀; NHMW).

Discussion.— Based on the subcontiguous procoxae, the four-segmented antennal funicle, obliquely truncate antennal club with first segment forming a circular costa and segment 1 covering most of the posterior face, the presence of a coarse median pair of asperities on the produced anterior margin of the pronotum, the protibiae with seven socketed teeth, and the elytra that are wider than long, this species is here transferred to *Cnestus*.

New Combinations, *Cyclorhipidion*

Cyclorhipidion squamulatum (Beaver and Löyttyniemi), new combination

Apoxyleborus squamulatus Beaver and Löyttyniemi, 1985:69. Holotype ♀: Zambia: Lusaka, 21.i.1980, light trap. R.A. Beaver coll; BMNH.

Xylosandrus squamulatus (Beaver and Löyttyniemi): Wood, 1984:229.

NOTES.— Beaver and Löyttyniemi (1985) described this species in the genus *Apoxyleborus*. However, Wood (1984) had synonymized *Apoxyleborus* with *Xylosandrus*. The species was listed in *Xylosandrus* by Wood and Bright (1992).

DISTRIBUTION.— **Afrotropical Region:** Zambia.

HOSTS.— Unknown.

SPECIMENS EXAMINED.— (2 ♀; 0 ♂) TYPE MATERIAL: Holotype *Apoxyleborus squamulatus* (♀; BMNH). Paratype *Apoxyleborus squamulatus*: Zambia, Lusaka, 2052, 8-9.v.80, R.A. Beaver, trap light (♀; RAB).

DISCUSSION.— Based on the contiguous procoxae, antennal club with segment 1 not forming a circular costa (type 3, Hulcr et al. 2007), and arched protibiae with eight socketed teeth, this species is herein transferred to *Cyclorhipidion*. This species was compared with the holotype of the type species of *Cyclorhipidion*: *C. pelliculosum*. The inclusion of this species, along with *Cyclorhipidion pelliculosum* Hagedorn, in the phylogenetic analysis of morphological data caused the strict consensus tree to become completely unresolved. Because *Cyclorhipidion* has not been confused historically with *Xylosandrus*, the genus was not included in the phylogenetic analysis.

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Appendicies

Appendix 1

Morphological character matrix of 43 characters for 75 species. Characters are their scores described in Materials and Methods.

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Amasa anomalus	1	0	0	0	1	0	2	1	0	3	1	0	0	0	0	2	0	0	0	?	1	0	1	1	1
A. bicostatus	1	0	1	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	1	2	1	0	1	1	1
A. cylindriformis	1	0	1	0	?	?	?	2	0	3	1	0	0	0	0	2	0	0	0	2	?	0	1	1	1
A. cylindrotomicus	1	0	0	0	1	0	2	0	0	0	1	0	0	0	0	2	0	0	0	2	0	0	0	1	1
A. fulgens	1	0	1	0	?	0	2	2	0	3	1	0	0	0	0	2	0	0	0	?	?	0	0	1	1
A. omissus	1	0	0	0	?	0	2	2	0	3	1	0	0	0	0	2	0	0	0	2	?	0	1	1	1
A. oralis	1	0	2	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	1	?	0	0	1	1	1
A. striatotruncatus	1	0	1	0	1	0	2	1	0	0	1	0	0	0	0	2	0	0	0	1	2	0	1	1	1
A. umbratulus	1	0	1	0	1	0	2	0	0	3	1	0	0	0	0	2	0	0	0	?	1	0	1	1	1
A. versicolor	1	1	1	0	1	0	2	2	0	3	1	0	0	0	0	2	0	0	0	2	1	0	1	1	1

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Amasa anomalus	1	1	2	1	2	0	0	0	2	0	0	2	1	2	0	0	0	0
A. bicostatus	1	1	2	1	1	0	0	0	0	?	?	0	1	0	?	?	1	1
A. cylindriformis	1	2	2	1	0	0	0	0	0	?	?	2	1	0	?	?	1	1
A. cylindrotomicus	1	1	2	1	1	0	0	0	0	?	?	1	1	0	?	?	0	0
A. fulgens	1	1	2	1	1	0	0	0	1	0	0	2	1	1	1	0	1	1
A. omissus	1	1	2	1	3	0	0	0	0	?	?	1	1	1	0	1	0	0
A. oralis	1	1	2	0	?	0	0	1	?	?	?	1	1	1	0	0	1	1
A. striatotruncatus	1	1	2	1	1	0	0	0	0	?	?	0	1	0	?	?	0	0
A. umbratulus	1	1	2	1	1	0	0	0	0	?	?	2	1	0	?	?	0	1
A. versicolor	1	1	2	1	1	0	0	0	0	?	?	2	1	0	?	?	0	1

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Anisandrus butamali	0	0	0	0	1	1	0	2	0	1	0	1	1	1	0	2	1	0	0	2	1	2	1	1	0
A. dispar	1	0	0	0	1	1	0	0	0	1	1	2	1	0	0	1	0	0	0	2	1	0	0	1	0
A. obesus	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	0	0	0	1	2	0	1	1	0
A. sayi	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	2	2	0	1	1	0
A. ursa	1	0	0	0	2	1	0	0	0	1	0	2	1	0	1	2	1	0	0	2	1	0	1	1	0
A. ursinus	1	0	0	0	2	1	0	0	0	1	1	1	1	0	1	2	1	0	0	2	1	0	1	1	0
A. ursulus	1	0	0	0	2	1	0	0	0	1	1	2	1	0	1	2	1	0	0	2	1	0	1	1	0

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Anisandrus butamali	1	2	1	1	0	0	0	0	?	4	0	0	0	0	?	?	1	1
A. dispar	1	0	0	1	0	0	0	1	?	4	0	0	0	1	0	1	1	1
A. obesus	2	0	1	1	0	0	0	3	?	4	1	0	0	1	0	1	1	0
A. sayi	2	0	1	1	0	0	0	1	?	4	1	0	0	0	?	?	1	0
A. ursa	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1
A. ursinus	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1
A. ursulus	1	0	1	1	0	0	0	0	?	3	0	0	0	0	?	?	1	1

Appendix 1 (continued)

Morphological character matrix of 43 characters for 75 species.
Characters are their scores described in Materials and Methods.

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cnestus ater	0	0	0	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	1	3	2	1	0	1
C. bimaculatus	0	2	0	0	0	1	0	1	0	1	1	0	1	0	1	1	1	0	1	1	0	2	1	1	0
C. fijianus	0	0	0	0	0	2	1	0	0	1	1	2	1	0	1	1	1	1	1	1	2	2	1	0	1
C. gravidus	0	0	0	0	0	2	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	2	1	1	1
C. improcerus	0	2	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0	1	2	1	0	1
C. laticeps	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1	2	1	0	1
C. mutilatus	0	0	2	1	0	2	1	0	0	1	1	2	1	0	1	1	1	1	1	1	2	2	1	0	1
C. orbiculatus	0	0	0	0	0	2	0	1	0	1	1	0	1	0	0	1	1	1	1	1	?	2	1	0	1
C. peruanus	1	0	0	0	0	1	0	0	0	1	1	2	1	0	1	1	1	1	0	1	1	0	1	1	0
C. pseudosolidus	0	0	0	0	0	2	0	1	0	1	1	1	1	0	0	1	1	0	0	1	0	2	1	1	1
C. pseudosuturalis	1	2	0	0	0	2	0	1	0	1	1	1	1	0	0	1	1	1	1	1	?	0	1	1	0
C. retifer	0	0	0	0	0	1	0	2	0	1	1	0	1	0	0	1	1	1	0	1	?	2	1	1	1
C. retusus	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	2	1	1	1
C. solidus	0	1	0	0	0	2	0	0	0	1	1	2	1	0	1	1	1	0	0	1	1	2	1	1	1
C. testudo	0	0	2	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	1	2	2	1	0	1
C. triangularis	1	0	0	0	0	2	0	2	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
Coccotrypes dactyliperda	1	0	2	0	0	2	1	2	1	0	1	2	0	1	1	0	?	0	0	2	0	0	0	1	0
Xyleborus affinis	1	0	0	0	1	2	1	2	0	0	1	1	0	0	0	0	?	0	0	2	0	0	0	1	0
X. californicus	1	0	0	0	1	2	1	2	0	0	1	1	0	0	0	0	?	0	0	2	2	0	0	1	0

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Cnestus ater	1	0	2	0	3	0	1	1	1	0	0	1	1	1	0	0	0	0
C. bimaculatus	0	0	2	0	3	0	0	0	0	?	?	0	1	0	?	?	0	0
C. fijianus	0	0	2	0	?	0	1	1	1	1	0	1	1	1	1	0	0	0
C. gravidus	0	0	2	0	3	0	0	0	1	1	0	1	1	1	1	0	1	0
C. improcerus	0	0	2	0	?	0	0	0	1	1	0	1	1	1	1	0	0	0
C. laticeps	0	0	2	1	?	0	0	1	0	?	?	1	1	0	?	?	0	0
C. mutilatus	1	0	2	0	?	0	0	1	1	1	0	1	1	1	1	0	0	0
C. orbiculatus	0	0	2	0	3	1	0	0	0	?	?	1	1	0	?	?	0	0
C. peruanus	0	0	2	0	3	0	0	0	1	1	1	1	1	1	1	1	1	0
C. pseudosolidus	0	0	2	0	4	1	0	0	1	?	0	1	1	1	1	0	0	0
C. pseudosuturalis	0	0	2	0	3	0	0	0	0	?	?	0	0	1	1	1	0	0
C. retifer	0	0	2	0	?	0	0	1	0	?	?	0	1	0	?	?	1	1
C. retusus	1	0	2	0	?	0	1	1	0	?	?	1	1	0	?	?	0	0
C. solidus	0	0	2	0	4	1	0	0	1	0	1	1	1	1	1	0	0	0
C. testudo	1	0	2	0	3	0	0	0	1	0	0	1	1	1	1	0	0	0
C. triangularis	0	0	2	0	3	0	0	0	?	?	?	1	0	1	1	1	0	0
Coccotrypes dactyliperda	0	0	0	?	?	0	0	0	1	0	0	1	0	1	1	1	0	0
Xyleborus affinis	0	0	1	?	4	0	0	0	0	?	?	1	0	1	1	1	0	0
X. californicus	0	0	0	?	4	0	0	0	1	0	1	1	1	1	1	1	0	0

Appendix 1 (continued)

Morphological character matrix of 43 characters for 75 species.
Characters are their scores described in Materials and Methods.

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Xylosandrus adherescens	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	0
X. amputatus	1	0	0	1	1	1	0	0	0	0	1	1	1	0	1	2	0	0	0	0	0	0	1	1	1
X. arquatus	1	1	?	0	?	1	0	0	1	0	1	1	1	1	0	2	0	0	0	0	0	0	0	1	0
X. assequens	1	0	2	0	1	1	0	0	0	0	1	1	0	0	1	2	0	0	1	0	0	0	1	1	0
X. beesoni	1	0	2	0	1	1	0	0	0	0	1	2	1	1	1	2	0	0	1	0	0	0	1	1	1
X. borealis	1	0	2	1	1	1	0	2	0	2	1	2	1	1	1	2	0	0	0	0	0	0	1	1	1
X. borneensis	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	1
X. brevis	1	0	2	1	1	1	0	0	0	0	1	2	1	1	1	2	0	0	0	0	0	0	1	1	1
X. compactus	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0	2	0	0	1	0	0	0	0	1	0
X. corthyloides	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	1	1
X. crassiusculus	1	0	2	0	1	1	0	1	0	0	1	2	1	0	1	2	0	0	0	1	0	0	1	1	0
X. curtulus	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	2	0	0	1	0	0	0	0	1	0
X. derupteterminatus	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	1
X. deruptulus	1	0	2	0	?	?	?	0	0	0	1	1	?	0	1	2	0	0	1	0	?	0	1	1	0

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Xylosandrus adherescens	0	0	2	0	4	1	0	0	0	?	?	1	0	1	1	0	0	0
X. amputatus	1	2	2	1	2	0	0	0	0	?	?	2	1	0	?	?	1	0
X. arquatus	0	0	2	0	4	0	0	0	1	1	1	0	0	1	0	1	0	0
X. assequens	0	0	2	0	4	0	0	0	1	1	1	1	1	1	1	1	0	0
X. beesoni	1	0	2	0	3	0	1	0	1	0	0	1	1	1	?	?	0	0
X. borealis	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
X. borneensis	0	0	2	0	4	1	0	0	1	0	0	1	1	1	0	1	1	0
X. brevis	1	0	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
X. compactus	0	0	2	0	4	0	0	0	1	0	0	0	0	1	3	1	0	0
X. corthyloides	1	1	3	?	3	0	0	0	1	1	1	1	1	1	1	1	0	0
X. crassiusculus	0	0	2	0	4	0	1	0	1	2	1	1	1	1	1	0	0	0
X. curtulus	0	0	2	0	4	0	0	0	1	0	0	1	0	1	1	1	0	0
X. derupteterminatus	0	1	2	0	3	0	0	0	0	?	?	1	0	1	0	1	0	0
X. deruptulus	0	0	2	0	4	0	0	0	?	?	?	1	0	?	?	?	0	0

Appendix 1 (continued)

Morphological character matrix of 43 characters for 75 species.
Characters are their scores described in Materials and Methods.

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
X. discolor	0	1	0	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0	0	1	1	1	1
X. diversepilosus	1	0	?	?	?	?	?	0	0	0	1	1	1	1	1	2	0	0	0	?	?	0	1	1	1
X. eupatorii	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0	2	0	0	1	0	0	0	0	1	0
X. ferinus	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0
X. germanus	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	1	0	0	0	0	1	0
X. hirsutipennis	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0
X. huleri	1	2	0	0	1	1	0	0	0	1	1	1	0	0	0	2	0	0	0	0	0	0	1	1	0
X. jaintianus	1	0	2	1	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0	0	0	1	1	1
X. mancus	1	3	0	0	1	1	0	1	0	0	1	1	1	0	0	2	0	0	0	0	0	0	1	1	1
X. mediocris	1	0	?	0	?	?	?	1	0	0	1	1	1	0	0	2	0	0	1	?	?	0	0	1	0
X. mesuae	1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	0	0	0	0	1	0
X. metagermanus	1	0	2	0	?	1	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	1	0
X. mixtus	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1	0	0	1	1	0
X. monteithi	1	0	0	0	1	1	0	0	0	1	1	2	0	0	0	2	0	0	0	0	0	0	1	1	0

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
X. discolor	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
X. diversepilosus	1	1	2	0	2	0	1	0	0	?	?	1	1	1	3	1	0	0
X. eupatorii	0	0	2	0	4	0	0	0	0	?	?	1	0	1	3	1	0	0
X. ferinus	0	0	2	0	3	0	0	0	0	?	?	1	0	1	0	1	0	0
X. germanus	0	0	2	0	4	0	0	0	0	?	?	1	0	1	1	1	0	0
X. hirsutipennis	0	0	2	0	3	0	1	0	1	1	0	1	1	1	1	0	0	0
X. huleri	0	0	2	0	3	0	0	0	1	0	1	1	1	1	1	1	0	0
X. jaintianus	1	2	2	0	2	0	1	0	1	0	0	1	1	1	0	0	1	0
X. mancus	1	1	2	1	2	0	0	0	0	?	?	1	1	0	?	?	1	0
X. mediocris	0	0	2	0	4	1	0	0	0	?	?	1	0	1	1	1	0	0
X. mesuae	0	0	2	0	4	0	0	0	1	0	0	1	0	1	1	1	0	0
X. metagermanus	0	0	2	0	4	0	0	0	0	?	?	1	0	1	1	1	0	0
X. mixtus	0	0	2	0	3	0	0	0	1	0	0	1	1	1	3	1	0	0
X. monteithi	0	0	0	?	4	0	0	0	1	1	0	1	1	1	1	0	0	0

	Characters																								
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
X. morigerus	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	2	0	0	1	0	0	0	0	1	1
X. pusillus	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	1	0	0	0	0	1	0
X. pygmaeus	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	1
X. queenslandi	1	0	2	0	1	1	0	0	0	1	1	1	1	0	0	2	0	0	0	0	0	0	0	1	1
X. rotundicollis	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1	1	0	1	1	0
X. russulus	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	2	0	0	0	1	2	0	1	1	0
X. subsimilis	1	0	2	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	1	0	0	0	1	1	1
X. subsimiliformis	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	2	0	0	0	0	0	0	1	1	1
X. terminatis	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	1
X. woodi	1	0	0	0	1	1	0	0	0	1	1	2	0	1	1	2	0	0	0	0	0	0	1	1	0

	Characters																	
Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
X. morigerus	0	0	2	0	4	0	0	0	1	0	1	0	0	1	3	1	0	0
X. pusillus	0	0	2	0	4	0	0	0	1	0	0	1	0	1	3	1	0	0
X. pygmaeus	0	1	2	0	3	1	0	0	0	?	?	1	0	1	1	1	0	0
X. queenslandi	0	1	3	?	4	0	1	0	1	0	1	1	0	1	1	1	0	0
X. rotundicollis	0	0	0	?	4	0	0	0	1	0	0	1	0	1	3	1	0	0
X. russulus	0	0	0	?	4	0	0	0	1	0	0	1	0	1	3	1	0	0
X. subsimilis	1	1	2	0	2	0	1	0	2	0	0	1	1	2	0	0	0	0
X. subsimiliformis	1	1	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0	0
X. terminatis	0	1	2	0	3	0	0	0	0	?	?	0	0	1	1	1	0	0
X. woodi	0	0	1	?	3	1	0	0	1	1	0	1	1	1	1	0	0	0

Appendix 2

Species data for morphological and molecular characters martricies
(● = data avaiable for species).

Species	Morphology	28S	COI	ArgK	CAD	EF-1α
Amasa anomalus (Schedl)	●					
Amasa bicostatus (Sampson)	●	●	●	●	●	●
Amasa cylindriformis (Schedl)	●					
Amasa cylindrotomicus (Schedl) n. comb.	●					
Amasa fulgens(Schedl)	●					
Amasa omissus (Schedl)	●					
Amasa oralis (Schedl)	●					
Amasa striatotruncatus (Schedl)	●	●	●	●	●	
Amasa umbratulus (Schedl)	●					
Amasa versicolor (Sampson)	●	●	●	●	●	●
Anisandrus butamali (Beeson) n. comb.	●					
Anisandrus dispar (Fabricius)	●	●	●	●	●	●
Anisandrus obesus(LeConte)	●	●	●	●	●	
Anisandrus sayi (Hopkins)	●	●	●	●	●	●
Anisandrus ursa (Eggers) n. comb.	●	●	●	●	●	●
Anisandrus ursinus (Hagedorn) n. comb.	●	●	●	●	●	●
Anisandrus ursulus (Eggers) n. comb.	●					

Species	Morphology	28S	COI	ArgK	CAD	EF-1α
Cnestus ater (Eggers), n. comb.	●	●	●	●	●	●
Cnestus bimaculatus (Eggers)	●	●	●	●	●	
Cnestus fijianus (Schedl) n. comb.	●					
Cnestus gravidus (Blandford) n. comb.	●					
Cnestus improcerus (Sampson) n. comb.	●	●	●	●	●	●
Cnestus laticeps (Wood) n. comb.	●					
Cnestus mutilatus (Blandford) n. comb.	●	●	●	●	●	●
Cnestus orbiculatus (Schedl) n. comb.	●					
Cnestus peruanus (Wood) n. comb.	●					
Cnestus pseudosolidus (Schedl)	●					
Cnestus pseudosuturalis Schedl	●	●	●	●	●	●
Cnestus retifer (Wood) n. comb.	●					
Cnestus retusus (Eichhoff) n. comb.	●					
Cnestus solidus (Eichhoff)	●					
Cnestus testudo (Eggers) n. comb.	●					
Cnestus triangularis (Schedl)	●					
Coccotrypes dactyliperda (Fabricius)	●	●	●	●	●	●
Xyleborus affinis Eichhoff	●	●	●	●	●	●
Xyleborus californicus Wood	●	●	●	●	●	●

Appendix 2 (continued)

Species data for morphological and molecular characters martricies
(● = data avaiable for species).

Species	Morphology	28S	COI	ArgK	CAD	EF-1α
Xylosandrus abruptulus (Schedl)	●					
Xylosandrus adherescens Schedl	●					
Xylosandrus amputatus (Blandford) n. comb.	●					
Xylosandrus arquatus (Sampson)	●					
Xylosandrus assequens Schedl	●					
Xylosandrus beesoni Saha, Maiti, & Chakraborti	●					
Xylosandrus borealis Nobuchi	●					
Xylosandrus borneensis n. sp.	●	●	●	●	●	●
Xylosandrus brevis (Eichhoff)	●					
Xylosandrus compactus (Eichhoff)	●	●	●	●	●	●
Xylosandrus corthyloides (Schedl)	●					
Xylosandrus crassiusculus (Motschulsky)	●	●	●	●	●	●
Xylosandrus curtulus (Eichhoff)	●					
Xylosandrus derupteterminatus (Schedl)	●					
Xylosandrus deruptulus (Schedl)	●					
Xylosandrus discolor (Blandford)	●	●	●	●	●	●
Xylosandrus diversepilosus (Eggers)	●					
Xylosandrus eupatorii (Eggers)	●					
Xylosandrus ferinus (Schedl)	●					
Xylosandrus germanus (Blandford)	●	●	●	●	●	●
Xylosandrus hirsutipennis (Schedl)	●					
Xylosandrus hulcr n. sp.	●	●	●	●	●	●
Xylosandrus jaintianus (Schedl)	●					
Xylosandrus mancus (Blandford)	●		●	●	●	●
Xylosandrus mediocris(Schedl)	●					
Xylosandrus mesuae (Eggers)	●					
Xylosandrus metagermanus (Schedl)	●					
Xylosandrus mixtus (Schedl) n. comb.	●					
Xylosandrus monteithi Dole & Beaver	●	●	●	●	●	●
Xylosandrus morigerus (Blandford)	●	●	●	●	●	●
Xylosandrus pusillus (Schedl)	●					
Xylosandrus pygmaeus (Eggers)	●					
Xylosandrus queenslandi Dole & Beaver	●	●	●	●	●	●
Xylosandrus rotundicollis (Browne) n. comb.	●	●	●	●	●	●
Xylosandrus russulus (Schedl) n. comb.	●	●	●			●
Xylosandrus subsimiliformis (Eggers)	●					
Xylosandrus subsimilis (Eggers)	●					
Xylosandrus terminatus (Eggers)	●					
Xylosandrus woodi Dole & Beaver	●					

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Geology at the California Academy of Sciences, 1853-1907

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In this paper, we use the technique of collective biography to document instances of those who used the California Academy of Sciences as the crucible in which to test new ideas developed during the California period of their scientific lives.

Geology at the California Academy of Sciences is a far-reaching topic, one that extends well beyond the confines of the assembling of collections and the organization of a department. It is more the people who associated themselves with the Academy for the purpose of exploring the problems usually thought of as geology or as one of the related disciplines. Thus, although from the early days of its existence, the Academy had a person designated a curator of mineralogy, and had a collection of minerals, said by some to be one of the finest in the state if not in the entire West, nevertheless, during the first 50 years of its existence, the main happenings in geology took place at the Academy's weekly or monthly meetings and in its publications.

To place geology in the proper context, it must be remembered that although incidental obser-

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[1] By 1853 the sciences of geology and paleontology were firmly established. In Europe the basic precepts of physical and historical geology had been brilliantly set forth in Charles Lyell's *Principles of Geology*, already in its eighth edition. The preparation of geological maps had become normal procedure. Stratigraphic and areal geology had been actively pursued since William Smith and Georges Cuvier had independently demonstrated the practical use of fossils, and the basic geological time scale had been established. Descriptive paleontology had been an active field for half a century, and Alcide d'Orbigny had established the basic principles and procedures of biostratigraphy, little changed to this day.

The main outlines of the geology and paleontology of the eastern United States had been elucidated by Conrad, Dana, Emmons, Hall, Hitchcock, Morton, Rogers and Rogers, Vanuxem, and others. By contrast, little was known of the geology and paleontology of western North America, and that little from scattered observations and collections made by voyages of discovery or exploring expeditions. (For these early efforts see articles by Addicott 1980, Alden and Ifft 1943, Anderson 1932, Jennings 1966, Natland 2003, and VanderHoof 1951, and bibliographies by Orr and Orr 1984, and Shedd 1932).

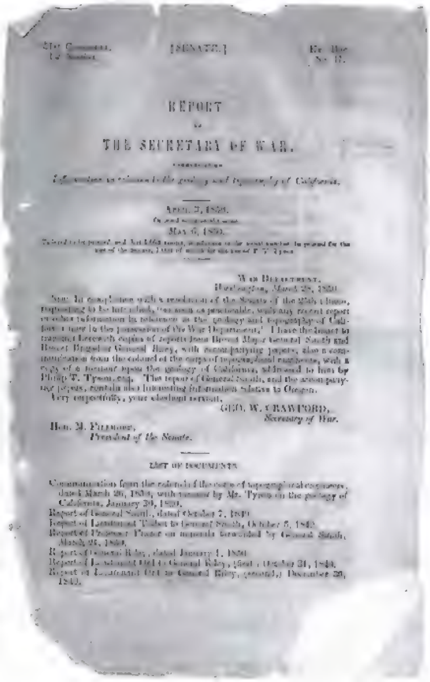
The earliest records are merely sightings of particular rocks or fossils, such as the fossil shells noted at Cape Blanco, Oregon in 1792 by Archibald Menzies during Vancouver's voyage to the northwest coast of North America, or the La Perouse voyage of 1791 that mentions what was probably one of the large fossil pecten shells from southeast Alaska (Addicott 1980).

On later expeditions, naturalists made geological observations and collected specimens of rocks and fossils for later study and possible publication. The Kotzebue voyage of 1816 to Alaska and California included the botanist, Adelbert von Chamisso, who made geological observations in the San Francisco area, and the zoologist, Johann Friedrich Eschscholtz, who collected samples of rocks and minerals later described by Moritz von Englehardt. Eschscholtz returned with Kotzebue's later voyage of 1823–1826, and made further zoological and geological collections which were described in his *Zoologischer Atlas* (1829–1833). On other explorations, the specimens collected were sent to various authorities for study. William Buckland in England received materials collected from California during the voyage of the *Blossom* in1831, and he (1839) prepared the geological section of the zoological report, which included a geologic map of the San Francisco Bay area, prepared by the ship's surveyor, Edward Belcher, and surgeon, Alex Collie, the first of its kind in the West. During his travels in the West, the botanist Thomas Nuttall sent fossils to T.A. Conrad in Philadelphia, who published on them in 1838. Bones found during Ewing Young's travels were sent to Boston and described by Henry C. Perkins (1842). The U.S. Exploring Expedition, and the Fremont expeditions sent geological specimens to James Hall (1845) in New York, and Fremont also sent samples of diatomaceous earth to the German diatomist Christian Gottfried Ehrenberg (1850, 1853).

The discovery of gold and mercury in California led to numerous publications (domestic and foreign) on California minerals and mining; nearly half of the pre-1853 publications cited in Shedd (1932) are on these subjects.

vations were made on the geology of California prior to the 1850s,[1] there was little incentive to do more until after the discovery of gold in 1848 and the resulting population explosion led people to want to know about the economic potential of their new home and the country of its new state.

California was admitted to the Union in 1850. As a prelude to this, in 1849, Philip Tyson (Fig. 1), who traveled to California as a privite citizen (Merrill 1964:290) reported on the peculiarities of the geology and industrial resources of the region to the War Department. His report was transmitted to Congress and published as a Senate Document in 1850. In 1851, two maps of the gold regions of California were printed, one by Charles Gibbes the other by William Jackson. And, in 1853, William Phipps Blake (Fig.2) prepared a geological map of the San Francisco Bay region for his Pacific Railroad report. But a more comprehensive report was that of John Boardman Trask (Fig. 3) who, in 1854, published a paper on the geology of the Sierra Nevada, and two maps, one of the State of California (Fig. 4) and the second, a topographical map of California's mineral districts (Fig. 5), the latter oriented with East on top and which, according to Wheat (1959:160) is not only one of the rarest but also "an outstanding map. . .". Trask published two additional reports on California geology in 1856 (1856a, 1856b).



[SENATE.]

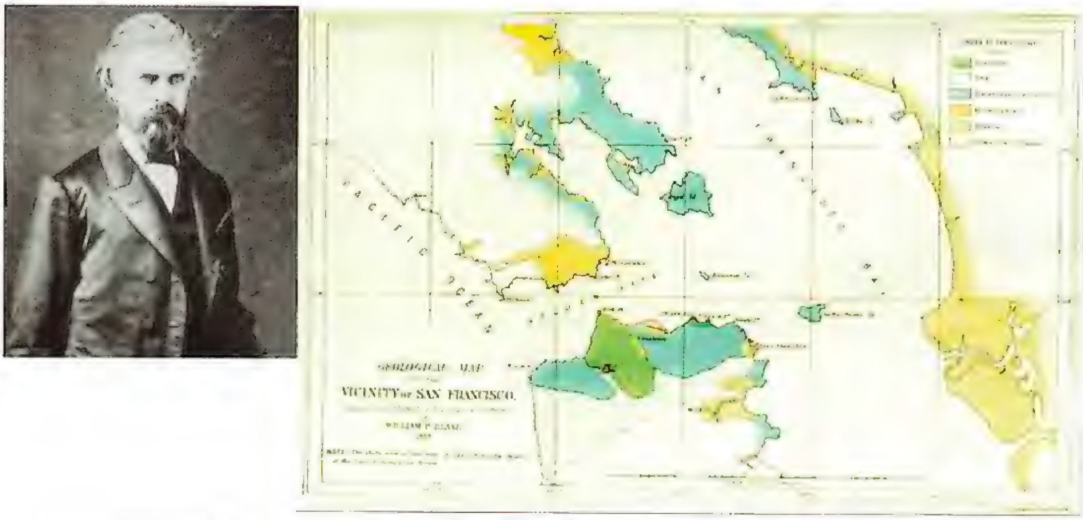
REPORT

THE SECRETARY OF WAR.

GEO. W. CRAWFORD,
Secretary of War.

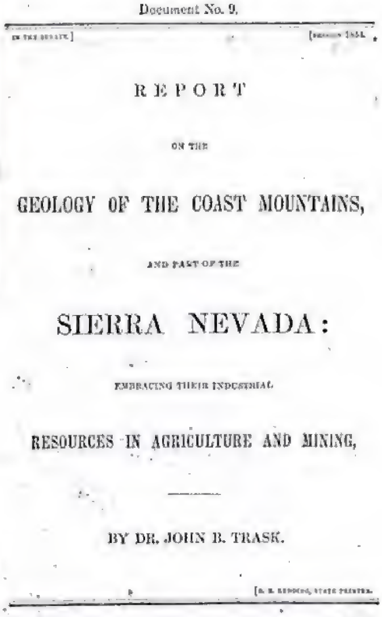
LIST OF DOCUMENTS.

FIGURE 1. Philip Tyson and the title/transmission page to his 1849 report on the geology of California. (See Acknowledgments for sources of images.)



FIGURES 2. William Phipps Blake and his 1853 geological map of the San Francisco Bay area.

At this time we take special note of Trask because he, with six other amateur naturalists, met on April 4, 1853 to found the California Academy of Natural Sciences. Of the seven people, two could claim some knowledge of geology, Trask and Andrew Randall (Fig. 6), the latter having earlier served as a field assistant to David Dale Owen on the Federal Survey of the Wisconsin-Minnesota territories. One month later, Leander Ransom (Fig. 7) joined them, and, not long thereafter, Pacific Railroad Survey geologist William Phipps Blake attended his first meeting the following January. Ransom was the federal surveyor responsible for establishing the Mount Diablo Base & Meridian line, the foundation for nearly all later topographic mapping done in northern California.



Document No. 9.

REPORT

ON THE

GEOLOGY OF THE COAST MOUNTAINS,

AND PART OF THE

SIERRA NEVADA:

EMBRACING THEIR INDUSTRIAL

RESOURCES IN AGRICULTURE AND MINING,

BY DR. JOHN B. TRASK.

FIGURE 3. John Boardman Trask and the title page of his 1854 Report on the Geology of California's Coast Ranges and Sierra Nevada, the first of three such reports submitted to the California State Legislature in which the economic potential of the State's resources is emphasized.

With the founding of the Academy, which at the time functioned more like a scientific society, members presented their latest observations on local natural history at weekly meetings. Also, local newspapers published verbatim transcripts of the talks. These included the *Daily Alta California* and *The Pacific* (Fig. 8), a Congregationalist weekly published in San Francisco. Somewhat later the *Mining and Scientific Press* and the *Placerville Times* followed suit. Copies of the newsprint columns were sent East, and among the recipients were Spencer Fullerton Baird and Joseph Henry (Fig. 9) of the Smithsonian Institution, which was then only seven years old.

Although both Henry and Baird were supportive of the fledgling Academy, it was Baird who advised its members that if they wanted to have their publications taken seriously "by men of science," they should publish the proceedings in journal format (Leviton and Aldrich 1997:33–34). Thus, in September 1854, the Academy issued the first four-page signature of volume 1 of the *Proceedings of the California Academy of Natural Sciences.*

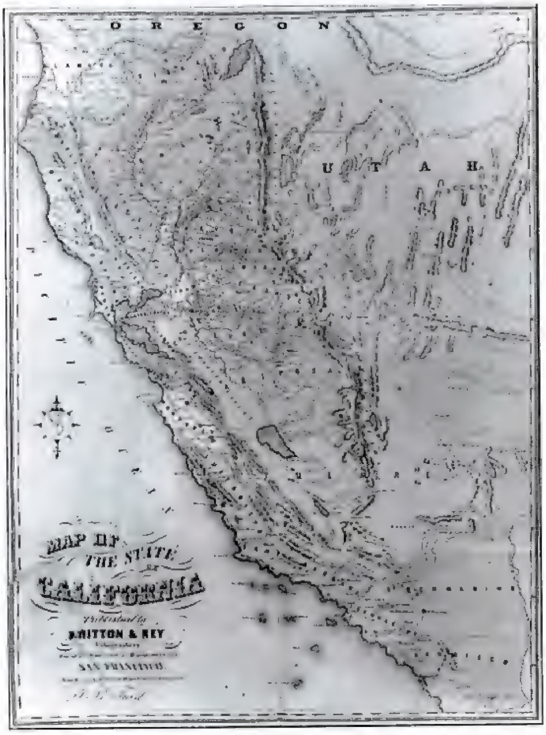


FIGURE 4. Trask's California map of 1853. (Courtesy of the Bancroft Library, University of California, Berkeley.)

With weekly meetings and an official publication, the Academy attracted new members and

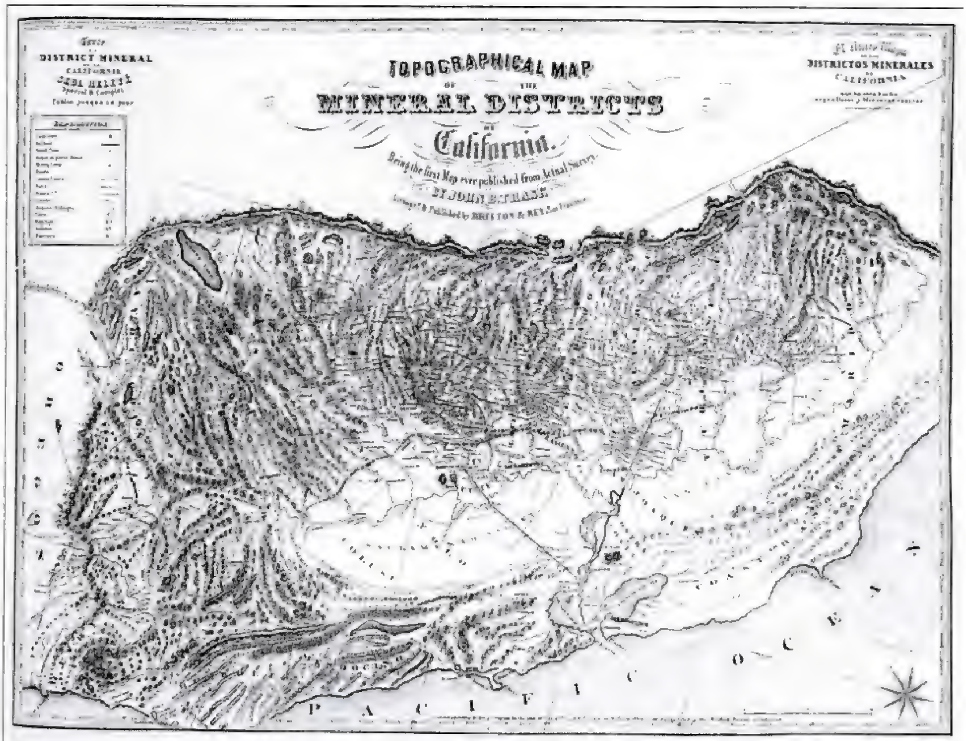


FIGURE 5. Trask's mining district map of 1853. (Courtesy of the Bancroft Library, University of California, Berkeley.)

FIGURE 6. Andrew Randall.

FIGURE 7. Leander Ransom.

provided a place where members could talk about scientific matters and, through the media, inform the public, who were welcome to attend the meetings, about local and regional natural history.

From its founding the Academy began a vigorous, though unsystematic, program to learn about, and acquire specimens of, the minerals, rocks, geology, and fossils of the vast, poorly known western North America, especially of the Pacific slope. Minutes of the early Academy meetings record varied geological observations and specimens brought for discussion and examination and for addition to the growing cabinet. For example, the minutes for 1854 record specimens of ferruginous earth from the San Francisco Bay area, asbestos in serpentine from Fort Point, crystalline limestone from Point Quentin, coal and sandstone from Puget Sound, salt from Isla Carmen (already indicating an Academy interest in Baja California), fossil bone from San Francisco, and a mastodon tooth from Sonora.

All of this reflected the excitement of discovery and the eagerness to share this newly-found knowledge through open meetings and publication of the proceedings. Although this type of small-

The Pacific.

FIGURE 8. Front page of *The Pacific*, the Congregationalist weekly newspaper published in San Francisco that regularly carried news about the Califonria Academy of Natural Sciences and its meetings.

scale observations by dedicated amateurs continued as the principal Academy activity for many years, major scientific contributions included John Boardman Trask's pioneering studies of California earthquakes.

FIGURE 9. (left) Spencer Fullerton Baird; (right) Joseph Henry.

Although the earliest papers on geological topics appeared in 1855, including one by Trask on *Ammonites batesi*, which established the first recognition of Cretaceous rocks in California, Trask's paper in 1856 (Fig. 10) is of particular interest because it is the first of a series in which he chronicled the earthquakes that occurred in California. During the next 13 years, Trask issued updates, several of which were then reprinted in the *American Journal of Science*. Trask's data were incorporated into a larger catalogue by Edward Singleton Holden (Fig. 21f), *A Catalogue of Earthquakes on the Pacific Coast, 1769–1897*, which was published in 1898. Thus, Trask, like so many who pioneer interesting branches of study, was overshadowed while credit goes to the encyclopaedists. (Leviton and Aldrich 1982; Rodda and Leviton 1983.)

During the years 1853 to 1860, perhaps best defined as the period of explorers, surveyors, and physician-naturalists, those who dominated in the earth sciences included Trask, William Phipps Blake, Leander Ransom, and Charles Frederick Winslow, the latter interested in the mechanics of earthquakes, tides, and the like as well as cultural anthropology.

In 1860, the California State Legislature authorized a State Geological Survey under the direction of Josiah Dwight Whitney (Fig. 11). Whitney headquartered in San Francisco and quickly assembled the support staff (Fig. 11), William Henry Brewer, William More Gabb, volunteer Clarence King, and others. The Whitney period at the Academy is marked by a dramatic broadening of interest in geology, and by an increase in the number of presentations and geological publications, especially by survey personnel but also by Trask, William P. Blake, and several of Whitney's correspondents, Auguste Rémond and Baron Ferdinand von Richthofen (Fig. 13).

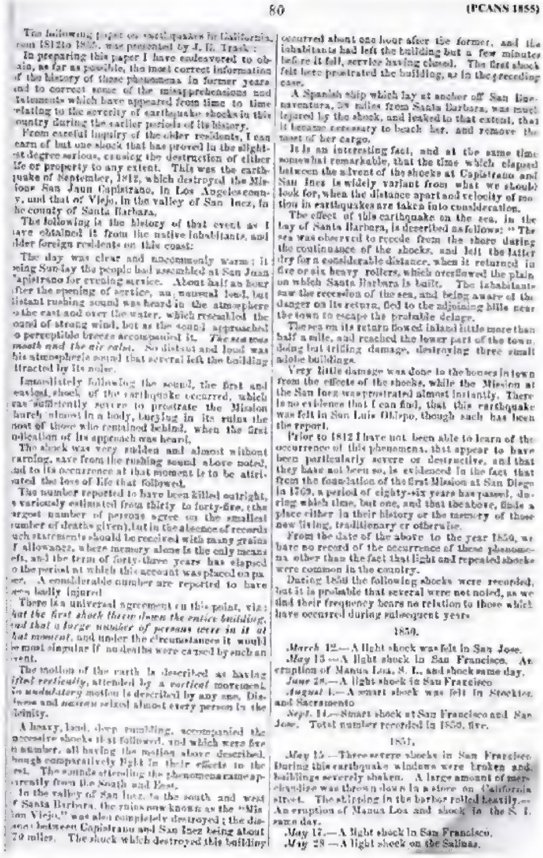


FIGURE 10. Trask's first paper cataloguing earthquakes in California, 1812 to 1855, published in PCANS 1:80-82 (volume for 1855 but published in 1856).

Among the topics addressed by the Whitney survey was the origin of the deep valleys of the Sierra Nevada, notably Yosemite and Hetch Hetchy. At the time, none appreciated the full impact of glacial erosion, a position John Muir (Fig. 12) posited some years later and for which he is given full credit. But it was not John Muir who first promoted the idea of significant glacial action in the Sierras; he was preceded by Joseph LeConte (*Proceedings* for 1873 and 1875) and James Blake (*Proceedings* 1875). Another quirk of history: with strong support from Academy members, Whitney convinced California's congressional delegation to propose legislation to set aside Yosemite as a national park in perpetuity for the benefit of the people, which was done when Abraham Lincoln signed the legislation in 1863, nine years before Yellowstone National Park was established during the Grant administration.

At this point Richthofen (Fig. 13) deserves notice because in 1868 Whitney, as Academy President, launched a new Academy publication series, the *Memoirs*, in which appeared Richthofen's *Principles of the Natural System of Volcanic Rocks*, a 45-page treatise on the classification of volcanic rocks. In 1892, Eduard Suess referred to Richthofen's classification (Fig. 14), also known as Richthofen's Series, as the one "welche Richthofen's scharfer Blick zuerst erkannte, deren Beständigkeit oft geleugnet worden ist. . ." (Suess 1883:220).

Also during the Whitney period, Watson Andrew Goodyear assembled materials for his important publication on coal mining in the state (1877) (Fig. 15); Goodyear was the Academy's first curator of geology (1866). Henry Garber Hanks, who became California's first State mineralogist, was appointed curator of mineralogy and began building one of the West's finest mineralogical collection. Notables such as James Dana and Benjamin Silliman Jr. published several mineralogical papers in the Academy's *Proceedings* (Dana 1864; Silliman Jr. 1867–1868), as did others (e.g., W.P. Blake 1857–1873; Jackson 1885–1886; Lindgren 1887–1890; Whitney 1863–1868).

In the mid-1860s, new people interested in the earth sciences appeared. Among the more

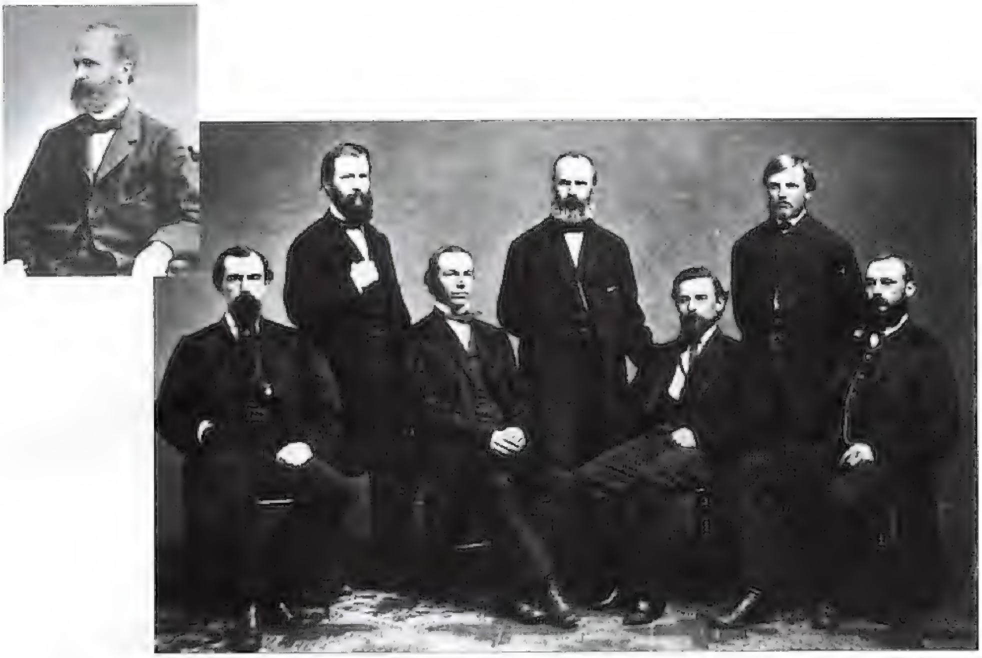
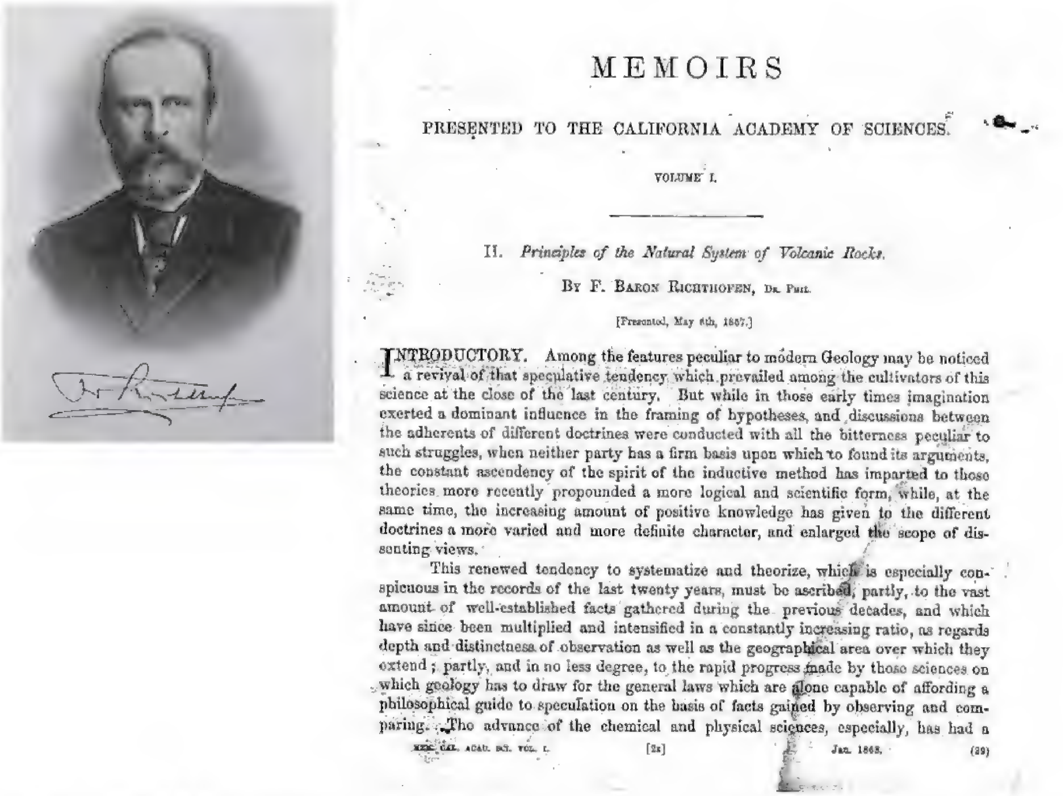


FIGURE 11. Josiah Dwight Whitney (insert upper left) and the members of the California Geological Survey, ca. 1862 (left to right) Chester Averill, William Gabb, William Ashburner, Josiah Whitney, Charles Hoffman, Clarence King, and William Brewer.

notable were William Healey Dall (Fig. 16) who had come West with the Western Union Telegraph's exploration and survey team to locate a route across Alaska to Siberia for a telegraph line; mathematician George Davidson (Fig. 17), who came to California as director of the Pacific Coast branch of the U.S. Coast Survey; Canadian geologist Amos Bowman (Fig. 18), who became interested in Bay area geomorphology, but then returned to the Geological Survey of Canada; and James Blake, M.D. (Fig. 19), previously a member of the Stansbury survey of the Great Salt Lake in 1849–1850, who came to California in 1850 and settled in Sacramento. Blake moved to San Francisco from Sacramento, where, for some time he had kept a low profile after his precipitous departure from Salt Lake City, just ahead of the sheriff, who had been sent by Brigham Young to recover property stolen from the Stansbury team. But that's another story!

FIGURE 12. John Muir, ca. 1863.

An interesting aside, based on the Coast Survey's hydrographic studies, is that both Dall and Davidson argued that the Japanese Warm Current did not enter the Bering Straits, as popularly thought, but that the Arctic circulation was internal and largely depended on tides and shallow water heating (Leviton and Aldrich 1997:144, 233). Because of the interest in opening a Northwest Passage, this was a crucial point and, in fact, it is likely that ignorance of this possibility led to the tragic loss of the U.S. Cutter *Jeannette* (Fig. 20) and its crew. (In all fairness to De Long and the crew of the *Jeannette*, it appears that neither Davidson nor Dall were present at the reception held on 16 June 1879 for the crew of the *Jeannette* [Leviton and Aldrich 1997:222–223, 514–515]).



MEMOIRS

PRESENTED TO THE CALIFORNIA ACADEMY OF SCIENCES.

VOLUME I.

II. *Principles of the Natural System of Volcanic Rocks.*

BY F. BARON RICHTHOFEN, DR. PHIL.

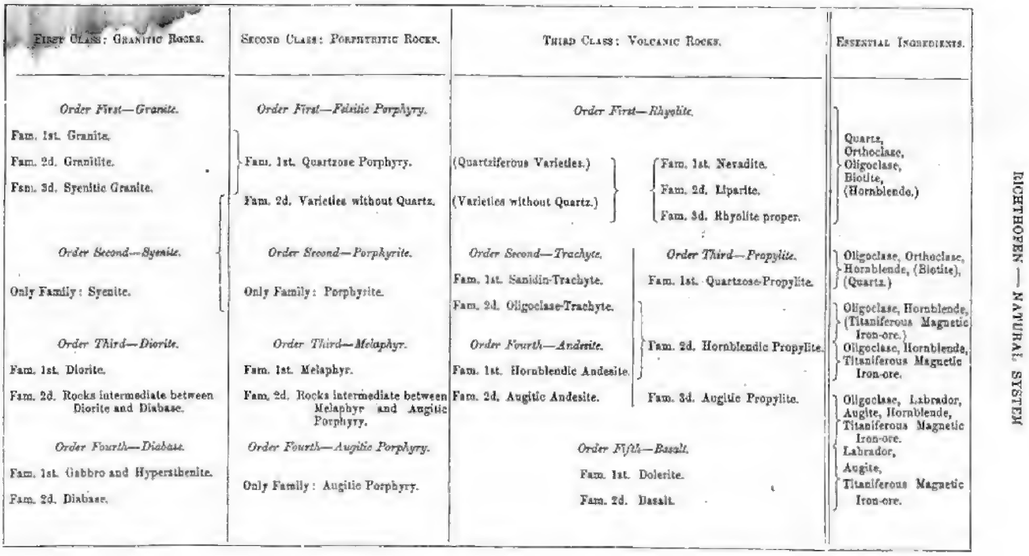
[Presented, May 6th, 1867.]

INTRODUCTORY. Among the features peculiar to modern Geology may be noticed a revival of that speculative tendency which prevailed among the cultivators of this science at the close of the last century. But while in those early times imagination exerted a dominant influence in the framing of hypotheses, and discussions between the adherents of different doctrines were conducted with all the bitterness peculiar to such struggles, when neither party has a firm basis upon which to found its arguments, the constant ascendency of the spirit of the inductive method has imparted to those theories more recently propounded a more logical and scientific form, while, at the same time, the increasing amount of positive knowledge has given to the different doctrines a more varied and more definite character, and enlarged the scope of dissenting views.

This renewed tendency to systematize and theorize, which is especially conspicuous in the records of the last twenty years, must be ascribed, partly, to the vast amount of well-established facts gathered during the previous decades, and which have since been multiplied and intensified in a constantly increasing ratio, as regards depth and distinctness of observation as well as the geographical area over which they extend; partly, and in no less degree, to the rapid progress made by those sciences on which geology has to draw for the general laws which are alone capable of affording a philosophical guide to speculation on the basis of facts gained by observing and comparing. The advance of the chemical and physical sciences, especially, has had a

MEM. CAL. ACAD. SCI. VOL. I. [2a] JAN. 1868. (29)

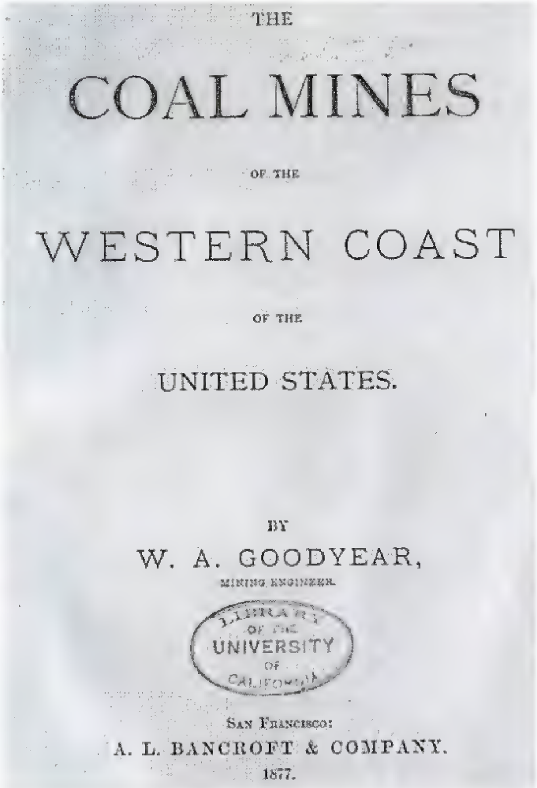
FIGURE 13. Richthofen's introduction to a classification of volcanic rocks published in 1868 in *Memoir* 1 of the California Academy of Sciences.



FIRST CLASS: GRANITIC ROCKS.	SECOND CLASS: PORPHYRITIC ROCKS.	THIRD CLASS: VOLCANIC ROCKS.		ESSENTIAL INGREDIENTS.
Order First—Granite.	*Order First—Felsitic Porphyry.*	*Order First—Rhyolite.*		Quartz, Orthoclase, Oligoclase, Biotite, (Hornblende.)
Fam. 1st. Granite.				
Fam. 2d. Granitite.	Fam. 1st. Quartzose Porphyry.	(Quartziferous Varieties.)	Fam. 1st. Nevadite.	
Fam. 3d. Syenitic Granite.	Fam. 2d. Varieties without Quartz.	(Varieties without Quartz.)	Fam. 2d. Liparite.	
			Fam. 3d. Rhyolite proper.	
Order Second—Syenite.	*Order Second—Porphyrite.*	*Order Second—Trachyte.*	*Order Third—Propylite.*	Oligoclase, Orthoclase, Hornblende, (Biotite), (Quartz.)
Only Family: Syenite.	Only Family: Porphyrite.	Fam. 1st. Sanidin-Trachyte.	Fam. 1st. Quartzose-Propylite.	
		Fam. 2d. Oligoclase-Trachyte.		Oligoclase, Hornblende, (Titaniferous Magnetic Iron-ore.)
Order Third—Diorite.	*Order Third—Melaphyr.*	*Order Fourth—Andesite.*	Fam. 2d. Hornblendic Propylite.	
Fam. 1st. Diorite.	Fam. 1st. Melaphyr.	Fam. 1st. Hornblendic Andesite.		Oligoclase, Hornblende, Titaniferous Magnetic Iron-ore.
Fam. 2d. Rocks intermediate between Diorite and Diabase.	Fam. 2d. Rocks intermediate between Melaphyr and Augitic Porphyry.	Fam. 2d. Augitic Andesite.	Fam. 3d. Augitic Propylite.	Oligoclase, Labrador, Augite, Hornblende, Titaniferous Magnetic Iron-ore.
Order Fourth—Diabase.	*Order Fourth—Augitic Porphyry.*	*Order Fifth—Basalt.*		
Fam. 1st. Gabbro and Hypersthenite.	Only Family: Augitic Porphyry.	Fam. 1st. Dolerite.		Labrador, Augite, Titaniferous Magnetic Iron-ore.
Fam. 2d. Diabase.		Fam. 2d. Basalt.		

RICHTHOFEN — NATURAL SYSTEM

FIGURE 14. Richthofen's classification of volcanic rocks.



THE

COAL MINES

OF THE

WESTERN COAST

OF THE

UNITED STATES.

BY

W. A. GOODYEAR,

MINING ENGINEER.

LIBRARY OF THE UNIVERSITY OF CALIFORNIA

SAN FRANCISCO:

A. L. BANCROFT & COMPANY.

1877.

FIGURE 15. Watson A. Goodyear on coal mines of the West Coast of the United States (1877). (From a copy in the University of California, Berkeley libraries.)

George Davidson's Pacific Coast hydrographic survey also led to the discovery of the deep submarine canyons off the central and southern California coast long before their presence was made popular by Francis Shepard (1941, 1948, 1966). As for others employed by Davidson, Thomas Jefferson Lowry deserves mention because of the instruments and mathematical approaches he devised for precise measurements of position at sea. Presented at Academy meetings, his papers were then published in the *Proceedings* (Lowrey 1875a, 1875b, 1875c), as were Davidson's papers on *Submarine Valleys of the Pacific Coast of the United States* (1886, 1897).

James Blake, who in 1868 followed Whitney as Academy President, took an interest in earthquakes, especially when the Haywards fault broke in 1868 and produced an earthquake some suggest was even more powerful than the 1906 San Francisco event. By analyzing patterns of destruction throughout the Bay region, Blake located the epicenter of the earthquake. In a separate article, he also speculated that there is a strong probability that elevation of land around the Bay Area is related to earthquakes whenever they occur (Blake 1863) (see also Aldrich et al. 1986). And, lastly, Blake would surely feel comfortable with present-day studies in Astrobiology inasmuch as he took great interest in the algae and other organisms that live at extreme temperatures in hot springs near Puebla, Nevada (Blake 1872a, 1872b, 1872c).

With the founding of the University of California in 1867 and Stanford University in 1891, a new breed of scientists appeared on the scene. The age of the amateur naturalist, however, competent, was fast drawing to a close. The age of professionalism, scientists trained in their disciplines, became the order of the day. At the Academy, it is often referred to as the "University period" because the meetings were dominated by university faculty and administration (Fig. 21): David Starr Jordan (Fig. 21a), President of Stanford, James Perrin Smith (Fig. 21b), whose Academy papers on ammonite ontogeny were pioneering efforts, Joseph LeConte (Fig. 21c), Edward Singleton Holden (Fig. 21f), A. Wendall Jackson (Fig. 21g), and Robert Edwards Carter Stearns (Fig. 21h), among others. They were joined by a new breed of professional geologists and engineers employed by the State and city of San Francisco: Waldemar Lindgren, Marsden Manson, whose interest in the glacial period led him to study the evolution of climates (Fig. 22), Harold Fairbanks, and, at the Academy, Frank Marion Anderson. Perhaps the most notable geological studies published in the Academy *Proceedings* in the late 19th century were those that dealt with Baja California, principally by Lindgren and by Academy naturalist and physician Gustav Eisen. But James Perrin Smith, John C. Merriam, and others also produced a steady stream of paleontological papers as did physician-naturalist James Graham Cooper, who had been associated with the Academy since his return to California from the Civil War. Cooper also served for a short time with the Whitney survey.

FIGURE 16. Wiliam Healey Dall ca 1865.

FIGURE 17. George Davidson

FIGURE 18. Amos Bowman.

FIGURE 19. James Blake

At this point we must digress and take note of the fact that several Academy members, e.g., Edward Booth, Edward S. Clark, James Graham Cooper, Edward T. Cox, and William Moore Gabb, were appointed to care for the limited paleontological collections that existed at the Academy during the 19th century (see Leviton and Aldrich 1997:62, 242, 252, 266, 283, 334, 414–415, 421). However, in 1903, Frank Marion Anderson (Fig. 23), who had become an Academy member in 1899, and who the year before had donated an important collection of fossils to the Academy, was appointed honorary curator of paleontology. The following year the appointment was [regular] curator of the Department of Paleontology, but again without salary. Anderson had amassed a significant collection of invertebrate fossils while engaged in stratigraphic studies in the Coalinga Oil District in Fresno County, California, and with ongoing field work elsewhere in California and Oregon, he built a large, comprehensive research collection of invertebrate fossils from the Late Mesozoic and Cenozoic rocks of the West Coast (see Leviton and Aldrich 1997:422, 425–426, 431–434, 453, 479). The large collections Anderson had amassed before 1906 were destroyed in the 1906 earthquake and fire, but he entered the gutted building before it was demolished, and was able to salvage a small collection of fire-damaged fossils, including some type specimens of ammonites he had described in 1902. Soon after the fire Anderson, with the help of his assistant, Bruce Martin, began to rebuild the fossil collections, and by 1916 they had re-established a major research collection when the Academy reopened in Golden Gate Park. As a result, since the period of his curatorship (1904–1917) geology at the Academy has been dominated by invertebrate paleontology.

In 1891, the Academy moved into its new museum building on Market Street (Fig. 24) that had been made possible by a major gift of James Lick in 1876. The building housed both research programs and public exhibits, among the latter being a large collection of exhibit-grade minerals and a spectacular mammoth reconstruction (Fig. 25) purchased from Henry Augustus Ward of Rochester, New York through the largess of Leland Stanford and Charles Crocker.

In the few pages available, we have sketched out broadly the Academy's participation in the earth sciences during the 53 years from its founding in 1853 to 1906 to give a sense of how it like-

FIGURE 20. 19th century images relating to the U.S.S. *Jeannette* and the Arctic expedition of 1879–1881.

ly influenced the lives and science of individual members. But on 18 April 1906 all that changed, at least for awhile, for on that day San Francisco and so many of its institutions, some holdovers from the heady days of the gold rush, were lost (Fig. 26) in the earthquake and ensuing fire. For the Academy, it was devastating; its collections, the finest natural history library west of the Appalachians, and its nearly new museum building — gone (Fig. 27). But not the people. And in so far as the earth sciences are concerned, several Academy members, for instance, Harold Wellman Fairbanks, John Casper Branner (Fig. 21e), David Starr Jordan, and others, such as Grove Karl Gilbert, wrote reports (Fig. 28) that were to reshape both public and governments' attitudes to earthquake hazards, building codes, and land use.

In summary, how does this story relate to the evolution of the Academy as a world-class research museum in the natural sciences? Academy geologists were educated elsewhere and transported their training to a new place that changed their thinking about the earth. James Blake, Whitney, and Richthofen were trained in England and Germany but found their theories reshaped by their Western experience. Trask had to cope with the phenomenon of earthquakes, largely foreign to an Eastern-trained naturalist. In many ways, these geologists affiliated with the Academy experienced the same transformation that the Irish geologists did on encountering India in the 1850s and 60s (Leviton and Aldrich 2000).

The Academy's function in the biographies of California geologists and naturalists in general also changed over time. For the explorer generation, it civilized San Francisco by adding a valuable cultural asset. For the survey generation, it offered a scientific, as opposed to a political, base of operations and an outlet for trying out new ideas and publishing short papers before the appearance of book-length reports. For the university period, the Academy was a place to mix with scientists from different schools and disciplines. In each era, one common thread is that it was not the

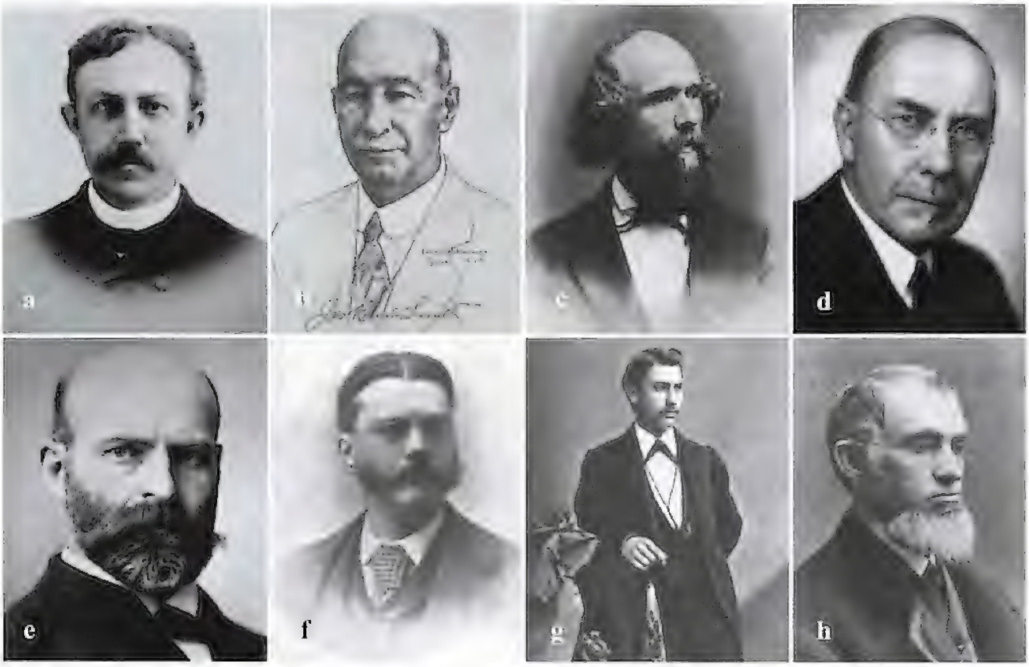
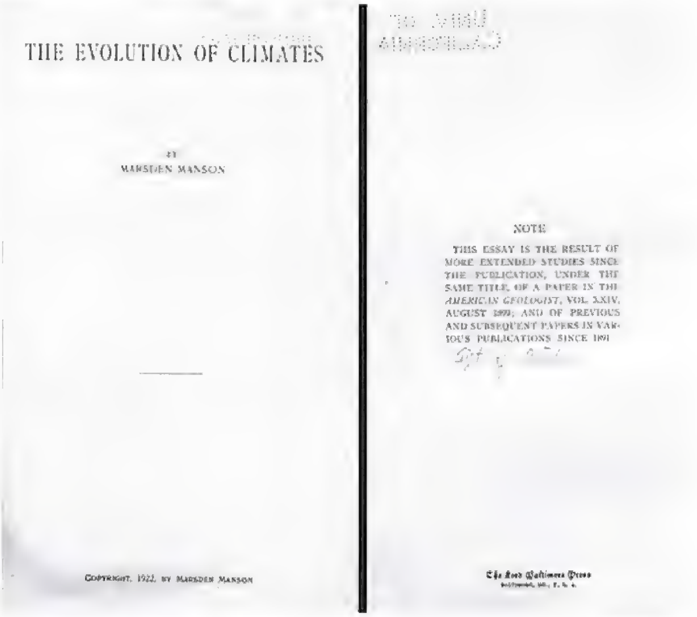


FIGURE 21. Dominant members of the Academy with interests in geology during the "University" period (left to right) upper row: (a) David Starr Jordan, (b) James Perrin Smith, (c) Joseph LeConte, (d) John C. Merriam; lower row: (e) John Branner, (f) Edward S. Holden, (g) A. Wendell Jackson, (h) Robert Stearns.

permanent home that academies provided for geologists in more settled districts. For many, it was a transient's place of support and fellowship.

Thus, first, and perhaps foremost, it provided a forum where people could meet, present papers, talk with colleagues and exchange views on topics of mutual interest, to be challenged, or just to socialize. Topics discussed and publications of importance that emerged from the meetings were often printed by the Academy (Fig. 29). The meetings must have been important to the members, even for those who subsequently may have denied its impact (e.g., LeConte quoted in M. Smith, 1987:219, fn. 22). For instance, Joseph LeConte from the University of California at Berkeley and David Starr Jordan from Stanford University in Palo Alto had to travel 40 and 80 miles roundtrip respectively to attend the meet-



THE EVOLUTION OF CLIMATES

BY
MARSDEN MANSON

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NOTE

THIS ESSAY IS THE RESULT OF MORE EXTENDED STUDIES SINCE THE PUBLICATION, UNDER THE SAME TITLE, OF A PAPER IN THE *AMERICAN GEOLOGIST*, VOL. XXIV, AUGUST 1899; AND OF PREVIOUS AND SUBSEQUENT PAPERS IN VARIOUS PUBLICATIONS SINCE 1891

The Lord Baltimore Press

FIGURE 22. Marsden Manson, 1922, *The Evolution of Climates*, based on papers published during the 1890s on the causes of the glacial epochs and climate change. (From a copy in the University of California, Berkeley libraries.)

ings, which were held in San Francisco. It must be remembered that this was before automobiles and San Francisco Bay bridges; thus, for LeConte it meant horse and buggy from Berkeley to Oakland, then a ferry to cross the bay, and a final three miles by trolley to the old Academy building at California and Dupont Streets or, after 1891, to 4th and Market Street; it was much easier for Jordan, a brief trolley ride from the Stanford campus to the train depot, about one mile, then a one hour 20 minute train trip up the Peninsula, and perhaps a 15 or 20 minute buggy ride to the Academy.

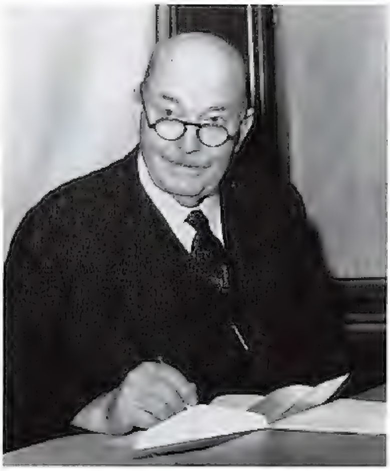


FIGURE 23. Frank Marion Anderson (1940).

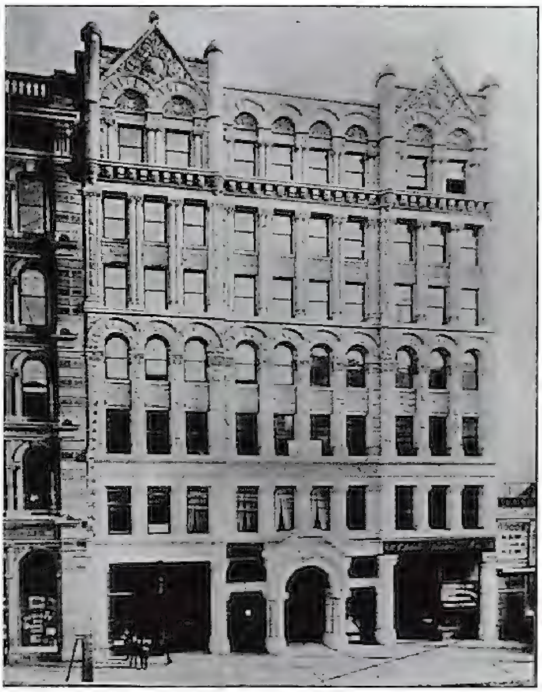


FIGURE 24. 1891. The Market Street building of the California Academy of Sciences. A second building, immediately behind and connected to the Market Street entrance by a bridge housed the museum, library, research collections, and Academy offices.

To compare with similar activities elsewhere, the California institution most closely resembles the Academy of Natural Sciences in Philadelphia, more so than the Smithsonian Institution, although in time both Academies were to open public museums, as did the Smithsonian. A notable difference between the Philadelphia and San Francisco organizations is that from the beginning the California Academy not only invited the public to participate but it made a special plea for women to get involved. And, well before 1900, it had four women on its salaried staff, three curators and the Academy librarian.

Second, it is clear from the publications record that during the latter half of the 19th century the Whitney and Davidson eras were peak periods for the presentation of papers in geology and earth sciences in general (Fig. 30).

Third, although the Academy did not publish all of the papers of its members, exchanges that took place at its meetings refined the presentations that ultimately were published. However, the Academy did publish some significant contributions in the earth sciences as noted earlier.

Finally, there were controversies not the least of which were Benjamin Silliman, Jr.'s claim on California diamonds, Whitney's negative views on the importance of oil in California and views on the origin of Yosemite Valley, and the fascinating history of the Carson City footprints, which involved both resident Academy members and members who lived elsewhere, such as Edward Drinker Cope, a member from 1888 until his death in 1897, and Othniel Charles Marsh. In all, the Academy proved a focal point for the collective biography of geologists who lived and worked in California, if only for part of their careers.

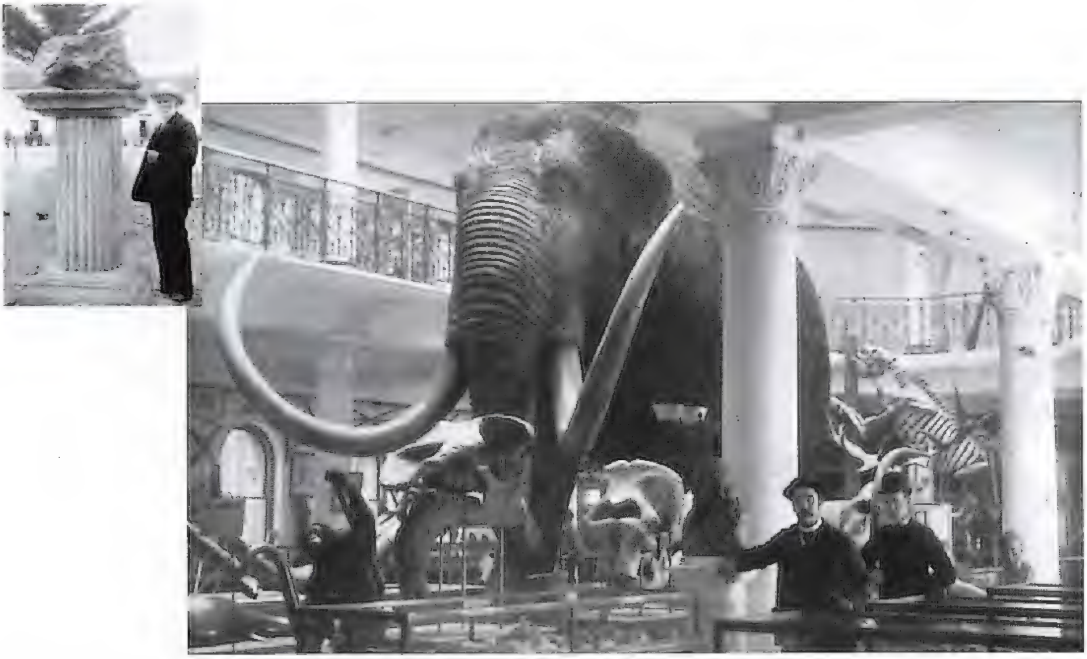


FIGURE 25. Ground floor of the museum building in 1892 with the Ward Mammoth as the centerpiece. Insert, upper left, Academy member and entrepreneur naturalist Henry Augustus Ward, founder of Wards Natural Science establishment in Rochester, New York.

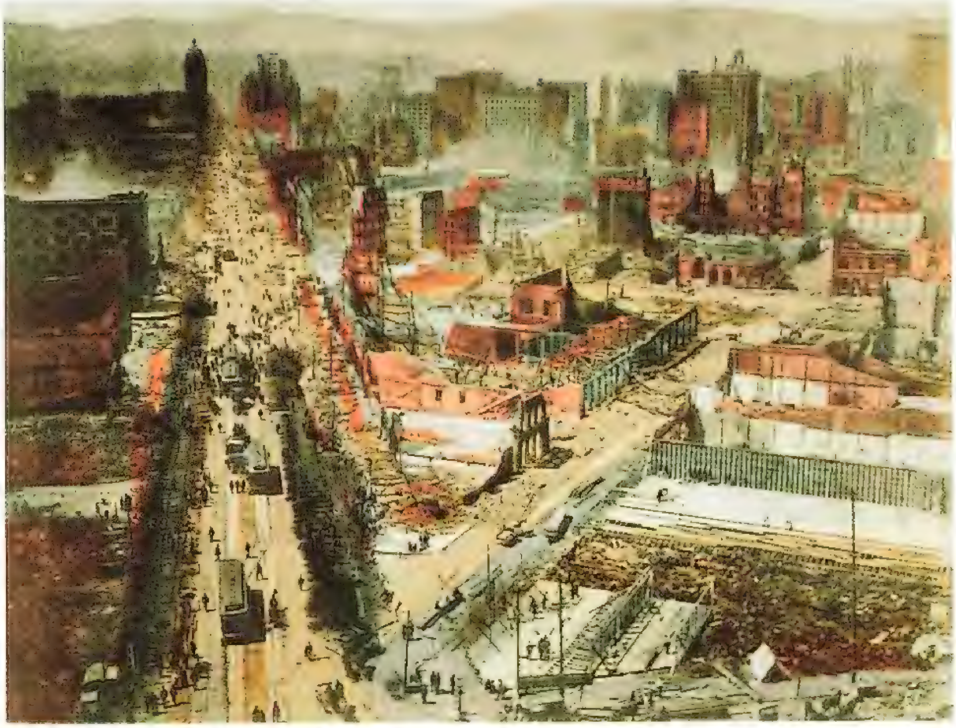


FIGURE 26. Downtown San Francisco following the earthquake and fire, 18 April 1906. Left, view up Market Street.

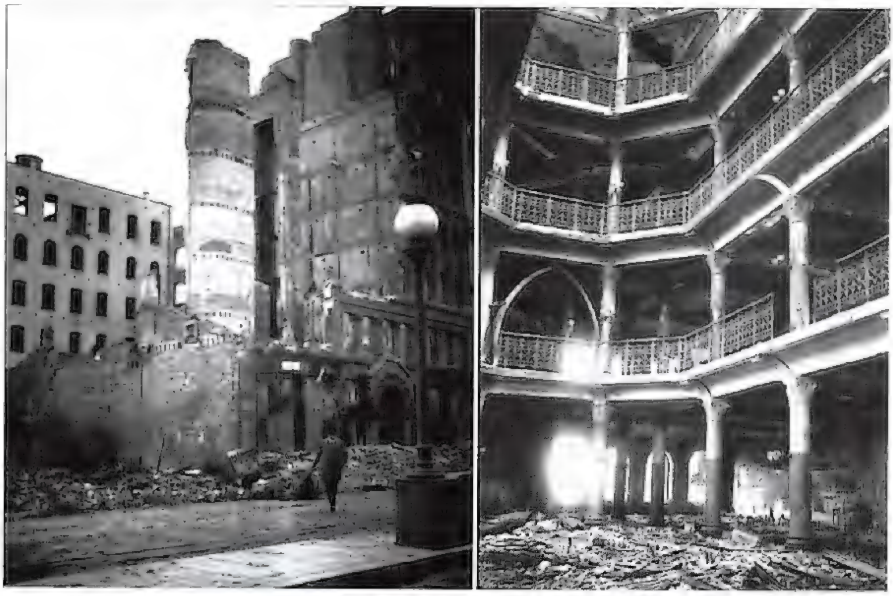
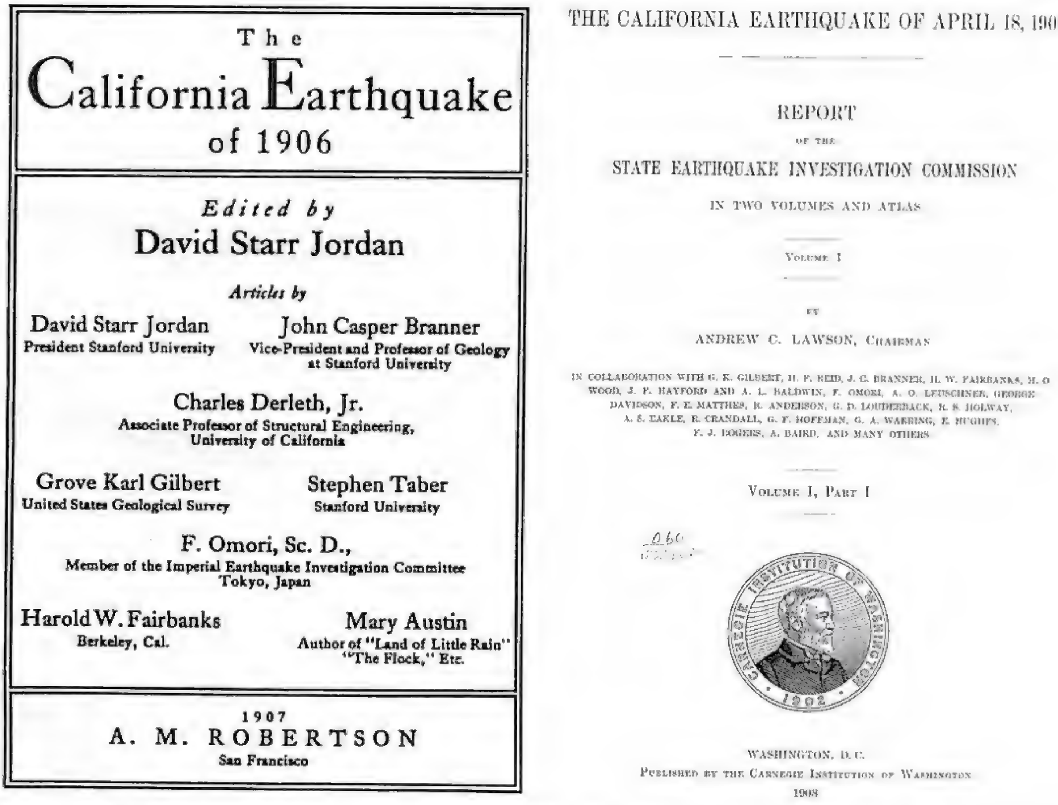


FIGURE 27. The California Academy of Sciences following the earthquake and fire, 18 April 1906. (left) Little remains of the front Market Street building; the white building on the left is all that remains of the Academy's museum. (right) The burned out interior of the Academy's museum building.



The
California Earthquake
of 1906

Edited by
David Starr Jordan

Articles by
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Mary Austin
Author of "Land of Little Rain" "The Flock," Etc.

1907
A. M. ROBERTSON
San Francisco

THE CALIFORNIA EARTHQUAKE OF APRIL 18, 1906

REPORT
OF THE
STATE EARTHQUAKE INVESTIGATION COMMISSION
IN TWO VOLUMES AND ATLAS

VOLUME I

BY
ANDREW C. LAWSON, CHAIRMAN

IN COLLABORATION WITH G. K. GILBERT, H. F. REID, J. C. BRANNER, H. W. FAIRBANKS, H. O WOOD, J. F. HAYFORD AND A. L. BALDWIN, F. OMORI, A. O. LEUSCHNER, GEORGE DAVIDSON, F. E. MATTHES, R. ANDERSON, G. D. LOUDERBACK, R. S. HOLWAY, A. S. EAKLE, R. CRANDALL, G. F. HOFFMAN, G. A. WARRING, E. HUGHES, F. J. ROGERS, A. BAIRD, AND MANY OTHERS

VOLUME I, PART I

060

1902

WASHINGTON, D. C.
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
1908

FIGURE 28. (left) *The California Earthquake of 1906*, edited by David Starr Jordan and published in 1907 preceeded the 1908 et. seq. Carnegie reports. (right) Title page of the California Earthquake Commission report.(1908).

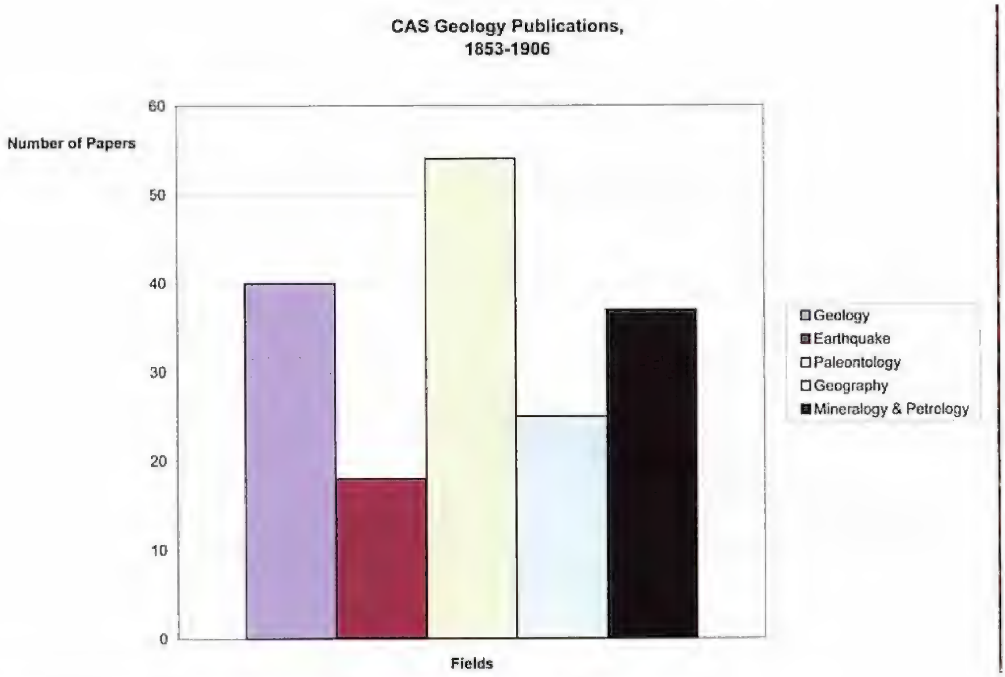
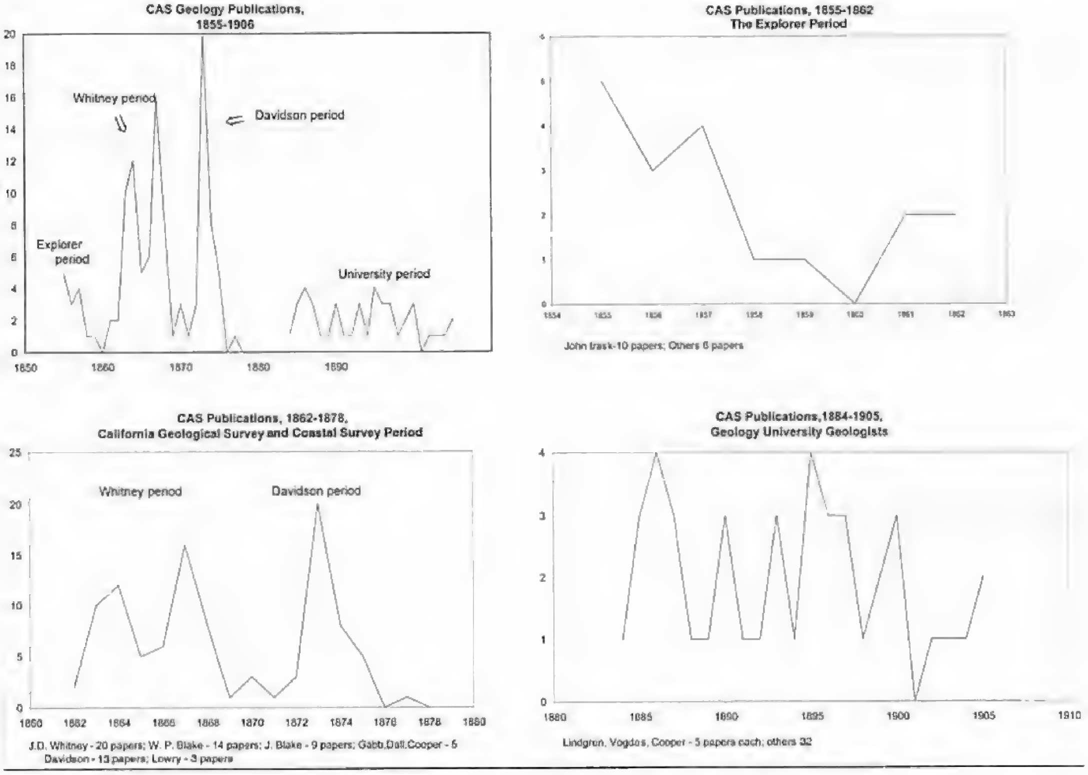


FIGURE 29. Academy publications in the earth sciences, 1854-1906, by discipline.



John trask-10 papers; Others 6 papers

J.D. Whitney - 20 papers; W. P. Blake - 14 papers; J. Blake - 9 papers; Gabb,Dall,Cooper - 5
Davidson - 13 papers; Lowry - 3 papers

Lindgren, Vogdes, Cooper - 5 papers each; others 32

FIGURE 30. Distribution of Academy publications in the earth sciences across the years 1854–1906.

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Individuals: Mark Aldrich, Ellen Alers, Patricia Akri, Alan Bain, Bruce Bolt†, Frank Carroll, William Cox, Larry Currie, Eunice Darvill, William Deiss†, J. Thomas Dutro, Jr.†, Clark Elliott, Karren Elsbernd, Tommie Ann Gard, Ferenc A. Gyprhyey, Peter Hanff, Pamela Henson, Anita Karg, Bruce Kirby, Thomas Moritz, Rebecca Pappert, Tammy Peters, Nathan Reingold†, Marc Rothenberg, Judith Schiff, Susan Snyder, Scott Stroh III, Benjamin Watson, Michele Wellck, Ellis Yochelson†, and others.

Unles otherwise noted in image legends or below, portraits are from the Archives, California Academy of Sciences or the GS Myers/AE Leviton Portrait and Biography File in the Natural Sciences. The following additional acknowledgments and thanks are extended to: Smithsonian Institution Archives (Figs. 1 [Philip Tyson], 3 [William Phipps Blake], 10a–b [Spencer Fullerton Baird and Joseph Henry], 12 [California State Geological Survey and insert of Josiah Dwight Whitney]; 15 [Richthofen insert]; 18 [William Healey Dall], 27 [H.A. Ward insert]); Bancroft Library, University of California, Berkeley (Figs. 23g [Wendell Jackson], 23h [Robert Carter Stearns]; Anacortes Museum, Anacortes, Washington (Fig. 20 [Amos Bowman]). Figure 22, a collage of images relating to the ill-fated voyage of the *Jeannette* (1879–1881) was assembled from images available online at the U.S. Navy Historical Center (*www.history.navy.mil/ photos/events/ev-1880s/jean-a.htm* [see also *jean-b.htm, -c, -d*, et seq, *-m*; also *jeannette.htm*]).

† Deceased.

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Phylogeography of the African Helmeted Terrapin, *Pelomedusa subrufa*: Genetic Structure, Dispersal, and Human Introduction

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The African Helmeted Terrapin, *Pelomedusa subrufa,* is currently recognized as a single species, and is found throughout sub-Saharan Africa, as well as on the Arabian Peninsula and in Madagascar. A preliminary genetic study of *Pelomedusa* based on mitochondrial and nuclear DNA is presented to determine the genetic diversity within *Pelomedusa*, and whether the disjunct populations are natural or anthropogenic. The monophyly of *Pelomedusa* is in question, as *Pelusios* may be nested within *Pelomedusa*. Within *Pelomedusa* there are three subgroups: Western, Eastern, and Southern. The Western clade is composed of two monophyletic groups divided by ecoregion, one through the Sahel region of Africa and the other in the savanna region of West Africa. The Eastern clade contains a disjunct population on the Arabian Peninsula, and divergence dating estimates indicate that this population was probably established through a natural dispersal event. The Southern clade includes a disjunct population in Madagascar, and this Malagasy population likely is the result of a recent human-mediated introduction, since sequence divergence compared to other individuals in the Southern clade is relatively low.

The African Helmeted Terrapin, *Pelomedusa subrufa,* is widespread over sub-Saharan Africa in semi-arid regions and savanna habitats (Loveridge 1941). *Pelomedusa* is a monotypic genus, and three subspecies are traditionally recognized, although there are some who have dismissed the validity of all three subspecies (Boycott and Bourquin 2008). In addition to continental Africa, there are two disjunct populations, one in Madagascar and another on the Arabian Peninsula, which are separated from the mainland by the Mozambique Channel and the Red Sea, respectively. The details surrounding the establishment of these disjunct populations are unknown; Malagasy and Arabian populations of *Pelomedusa* may be the result of a natural event or human introduction.

Pelomedusa subrufa is expected to be genetically diverse since other vertebrates with pan-African distributions show high levels of genetic structure (lizards of the genus *Agama* [Leaché et al. 2009] and bats of the genus *Otomops* [Lamb et al. 2008]). Within *Agama*, three regional clades were recovered (East, West, and South) with evidence of a Sahel radiation within the Western clade and a "biogeographic corridor" between East and West Africa (Leaché et al. 2009). Lamb et al. (2008) recovered three well-supported bat clades: a northeastern Africa including Yemen, an African clade excluding the northeast, and a Malagasy clade.

This and a concurrent study (Vargas-Ramirez et al. 2010) are the first to investigate the genetic structure within *Pelomedusa* across its range. By studying *Pelomedusa* genetically, we can gather preliminary data on genetic diversity, infer patterns of distribution, and test the validity of populations in Madagascar and the Arabian Peninsula. In this paper, a phylogeographic study of

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Pelomedusa subrufa is presented based on mitochondrial (*12S* rRNA, *16S* rRNA, *CytB* and *CO1*) and nuclear (1097 bp from RNA fingerprint protein 35 intron 1) DNA.

1. MATERIALS AND METHODS

1.1 Taxon Sampling and Laboratory Protocols

A total of 25 specimens were sequenced for this study, of which 19 are *Pelomedusa subrufa* and six are outgroup samples (one *Erymnochelys madagascariensis*, two *Platemys platycephala*, and three *Pelusios castaneus*). Previous to our work, only two known-locality *Pelomedusa* were sequenced and available on GenBank, both which we include in our analyses. Details on these specimens, including GenBank numbers, can be found in Table 1.

Total cellular DNA was extracted using a standard salt extraction protocol (Sambrook and Russell 2001). Four mitochondrial loci (12S rRNA [*12S*], 16S rRNA [*16S*], cytochrome b [*CytB*], and cytochrome oxidase 1 [*CO1*]) and one nuclear locus (RNA fingerprint protein 35 [*R35*]) were sequenced using the primer pairs indicated in Appendix I. For some samples where the DNA was degraded, internal primers were developed (Appendix II) to allow amplification of smaller, overlapping segments of the chosen genes. The samples were PCR amplified using standard thermocycler conditions. PCR amplified products were purified with ExoSAP-IT (USB Corp.) or gel extracted and purified using the Gel-ase enzyme (EPICENTRE Biosystems) when multiple products were amplified. The purified PCR products were cycle-sequenced using Big Dye Terminator v.3.1, and then sequenced using an ABI 3730 automated sequencer.

1.2 Phylogenetic Analysis

Sequencher v. 4.7 (Gene Codes) was used to align and edit complementary sequences. Multiple sequence alignments were generated using Muscle v3.7 (Edgar 2004).

Phylogenetic analyses were run on three different datasets: *R35* only (nuclear locus), combined mitochondrial loci (*12S, 16S, CO1, CytB*), and combined mitochondrial and nuclear loci. Datasets were partitioned by gene and codon position to account for different models of evolution (Brandley et al. 2005). Each dataset was analyzed under maximum likelihood (ML) using RAxML (Stamatakis et al. 2008) and Bayesian inference (BI) using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). ML analyses were run under the GTRMIX model of substitution and 1000 bootstrap replicates. For BI analyses, models of nucleotide substitution for each partition were estimated using MrModeltest v2.3 (Nylander 2004). Tests of stationarity were run with the online program AWTY (Wilgenbusch et al. 2004), and the appropriate burn-in was removed before combining runs.

1.3 Divergence Dating Analyses

The problems associated with divergence dating have been highlighted (Graur and Martin 2004; Parham and Irmis 2008). We heed their warnings and use conservative divergence dating methods to estimate separation times of the Arabian and Malagasy populations from the mainland. We calculated divergence dates using two methods, first by incorporating uncertainty from the geologic column into our fossil calibration date in BEAST v1.5.2 (Drummond and Rambaut 2007), and next by using a rate of evolution (Weisrock et al. 2001).

BEAST was run on the combined mitochondrial and nuclear dataset, partitioned by gene and codon, and run for 20 million generations. An uncorrelated log-normal clock model was used along with a speciation yule process tree prior and a normal prior frequency distribution. A fossil *Pelusios* (Williams 1954) was used as a calibration point for the divergence between *Pelusios-Pelomedusa* (Near et al. 2005), whose minimum divergence time is estimated to be 23.1-15.9 mya (Parham and Irmis 2008).

TABLE 1. Locality data, voucher numbers, and GenBank accession numbers for specimens used in this study. Detailed locality data can be obtained from the institutions. MVZ=Museum of Vertebrate Zoology, ULM=University of Louisiana at Monroe, R=Museum of Comparative Zoology, FGZC= Frank Glaw Zoological Collection, LSU=Louisiana Sate University, ZFMK= Zoologiches Forschungs Museum Alexander Koenig.

Species	Voucher #	Locality	12S	16S	CO1	CytB	R35
1) *Platemys platycephala*	MVZ 247579	Suriname	GU213780	GU213801	GU213826	GU213842	GU213861
2) *Platemys platycephala*	MVZ 247580	Suriname	GU213781	GU213802	n/a	GU213843	n/a
3) *Erymnochelys madagascariensis*	MVZ 238759	Madagascar	GU213782	GU213803	n/a	GU213844	GU213862
4) *Pelusios castaneus*	MVZ 250330	Sierra Leone	GU213783	GU213804	n/a	n/a	n/a
5) *Pelusios castaneus*	MVZ 250331	Sierra Leone	GU213784	GU213805	n/a	n/a	GU213863
6) *Pelusios castaneus*	ULM 178	Guinea	GU213785	GU213806	n/a	n/a	GU213864
7) *Pelomedusa subrufa*	R-184287	Namibia	GU213786	GU213807	n/a	GU213845	GU213865
8) *Pelomedusa subrufa*	FGZC 324	Madagascar	GU213787	GU213808	n/a	GU213846	GU213866
9) *Pelomedusa subrufa*	LSU 20145	Ghana	GU213788	GU213809	GU213827	n/a	GU213867
10) *Pelomedusa subrufa*	LSU 20315	Ghana	GU213789	GU213810	GU213828	n/a	GU213868
11) *Pelomedusa subrufa*	MVZ 245226	Ghana	GU213790	GU213811	GU213829	GU213847	GU213869
12) *Pelomedusa subrufa*	MVZ 245229	Ghana	GU213791	GU213812	GU213830	GU213848	GU213870
13) *Pelomedusa subrufa*	MVZ 238878	Niger	GU213792	GU213813	GU213831	GU213849	GU213871
14) *Pelomedusa subrufa*	MVZ 238879	Niger	GU213793	GU213814	GU213832	GU213850	GU213872
15) *Pelomedusa subrufa*	MVZ 238883	Niger	GU213794	GU213815	GU213833	GU213851	GU213873
16) *Pelomedusa subrufa*	MVZ238887	Niger	GU213795	GU213816	GU213834	GU213852	GU213874
17) *Pelomedusa subrufa*	MVZ 236628	Yemen	GU213796	GU213817	GU213835	GU213853	GU213875
18) *Pelomedusa subrufa*	MVZ 241329	Somalia	GU213797	GU213818	GU213836	GU213854	GU213876
19) *Pelomedusa subrufa*	MVZ 241330	Somalia	GU213798	GU213819	GU213837	GU213855	GU213877
20) *Pelomedusa subrufa*	MVZ 241331	Somalia	GU213799	GU213820	GU213838	GU213856	GU213878
21) *Pelomedusa subrufa*	MVZ 241332	Somalia	GU213800	GU213821	GU213839	GU213857	GU213879
22) *Pelomedusa subrufa*	ZFMK 15171	Cameroon	n/a	GU213822	GU213840	GU213858	n/a
23) *Pelomedusa subrufa*	ZFMK 17076	Senegal	n/a	GU213823	GU213841	GU213859	n/a
24) *Pelomedusa subrufa*	ZFMK 19836	Nigeria	n/a	GU213824	n/a	GU213860	n/a
25) *Pelomedusa subrufa*	ZFMK 54523	Malawi	n/a	GU213825	n/a	n/a	n/a
26) *Pelomedusa subrufa*	GENBANK	Ghana	DQ283264	DQ283264	n/a	n/a	n/a
27) *Pelomedusa subrufa*	GENBANK	Togo	n/a	AF113639	AF113663	n/a	n/a

Weisrock et al. (2001) reviewed the rate of evolution of mitochondrial DNA in a fragment including *ND1*, *ND2* and *CO1* and found it was consistent in a range of vertebrates at a rate of 0.57-0.69% per lineage per million years. Although there were no empirical data on turtles, we calculate divergence dates by applying the fastest rate (0.69% per lineage; 1.38% pair-wise rate) to our *CO1* dataset to obtain a minimum date of divergence.

2. RESULTS

Of the 2180 bp of mitochondrial DNA (*12S*, *16S*, *CytB*, *CO1*) sequenced, 591 sites were phylogenetically informative, while 70 of the 1097 bp of nuclear DNA (*R35*) were phylogenetically informative. Since some of the tissue samples were old or degraded, we were unable to compile a complete dataset. However, we were able to maintain our geographic coverage by sequencing a minimum of two mitochondrial markers for each sample. Although missing data may be a problem, our results seem relatively robust, as all phylogenetic analyses produced similar phylogenies. Herein, we only present the results of the ML analysis performed on the concatenated mitochondrial and nuclear dataset (Fig. 1). The monophyly of the family Pelomedusidae (*Pelomedusa* and *Pelusios*) is strongly supported (ML bootstrap = 99%; posterior probability = 1.0). Within *Pelomedusa* three geographic clades appear: Western, Eastern, and Southern (Figs. 1 and 2). Total variation between these three major clades of *Pelomedusa* is at most an uncorrected pair-wise difference of ~15% (mtDNA). However, the monophyly of the genus *Pelomedusa* is equivocal due to the position of *Pelusios*. *Pelusios* is either the sister group to the Southern *Pelomedusa* clade in the combined data analyses (weakly supported, Fig. 1), or forms an unresolved polytomy with the Southern and Eastern + Western *Pelomedusa* clades in our *R35* analyses (not shown).

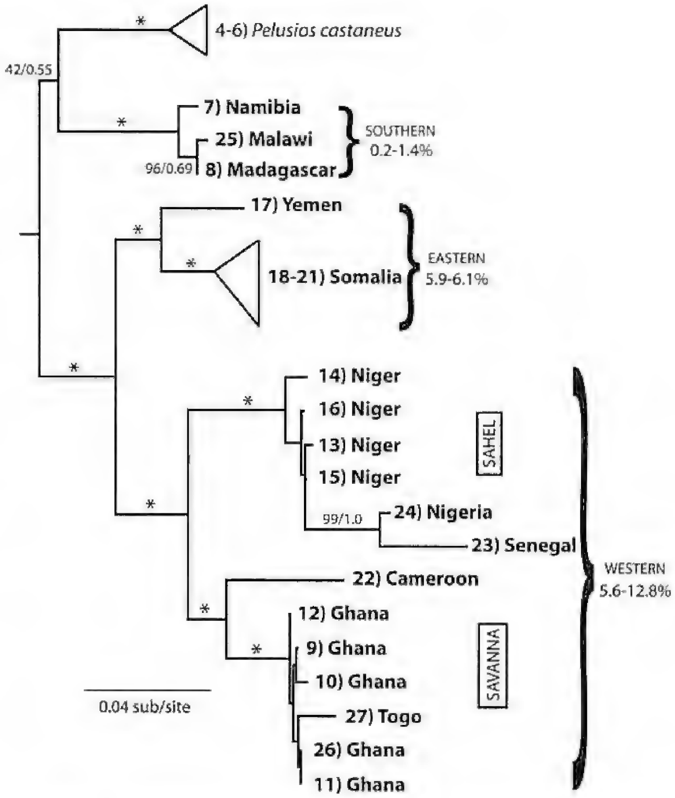

FIGURE 1. Phylogenetic inference from the maximum likelihood (ML) analysis on the combined mitochondrial and nuclear DNA analysis. ML and Bayesian analyses on mitochondrial only and nuclear only datasets produced similar trees. Support values on nodes are ML bootstraps/Bayesian posterior probabilities, while stars (*) represent full support (100/1.0). *Pelomedusa* clades are labeled according to the text and Figure 2. Ranges of percentages next to clades represent the uncorrected pair-wise sequence divergence between important specimens in the group—Southern: Madagascar and southern Africa, Eastern: Yemen and eastern Africa, Western: Sahel and Savanna. Numbers next to taxa correspond to the numbers in Table 1 and Figure 2.

2.1 The Western Clade

The Western clade consists of samples from Ghana, Togo, Cameroon, Niger, Nigeria, and Senegal (Fig. 1). Within this clade, there is further substructure, with one group consisting of Cameroon, Ghana, and Togo, and a second group consisting of Niger, Nigeria, and Senegal. These two groups differ by an uncorrected pair-wise difference of ~5.6–12.8%.

2.2 The Eastern Clade

The Eastern clade consists of individuals on the Horn of Africa (Somalia) and on the Arabian Peninsula (Yemen). There is strong support for this group from all phylogenetic analyses (ML bootstrap = 100%, Bayesian posterior probability = 1.0, Fig. 1). There is approximately 300km, including the Red Sea, between Somali and Yemeni specimens. The minimum sequence divergence between the Yemen and Somali specimens is 0.8% (*R35*) and 5.9% (mtDNA).

2.3 *The Southern Clade*

The Southern clade consists of samples from Malawi, Namibia, and Madagascar. In all cases, the Madagascar specimen is nested within the Malawi and Namibia specimens (ML bootstrap = 100%; Bayesian posterior probability = 1.0, Fig. 1). This is despite the long geographic distance (800-1600km) and the crossing of the Mozambique Channel. The percentage sequence divergence between the Madagascar individual and the other members of the Southern clade is ~0.4% (*R35*) and 0.5–1.4% (mtDNA).

2.4 *Divergence Dating*

Plots of likelihood scores indicated that BEAST analyses had reached stationarity. The *Pelomedusa* populations of particular interest are the disjunct populations in Yemen and Madagascar. 95% confidence intervals of the divergence dates were large, 14.1–0.8 mya for Yemen + Eastern Africa and 10.1–0.0006 mya for Madagascar + Southern Africa.

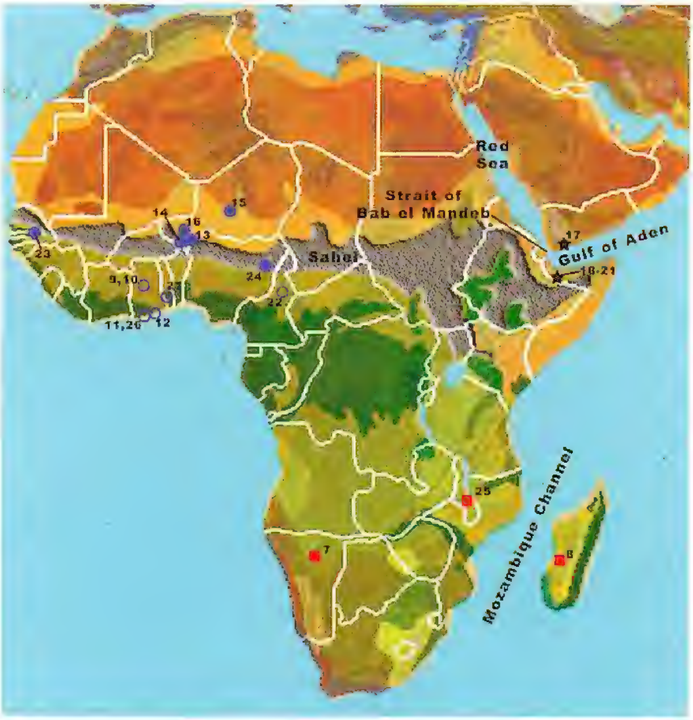

FIGURE 2. Map of specimen localities used in this study. Shapes correspond to the genetic clades found in Figure 1. Circles represent the Western clade, with filled-in circles representing samples in the Sahel and empty circles representing samples in the Savanna. Red squares represent the Southern clade and black stars represent the Eastern clade. Numbers next to taxa correspond to the numbers in Table 1 and Figure 1

For analyses using a 1.38%/million years rate of sequence evolution, we were able to calculate the divergence time of the Yemen sample, but not the Madagascar sample, as *CO1* sequences were unavailable for Madagascar and southern Africa samples. The percent sequence divergence between Yemen and Somalia was a minimum of 4.3%. By dividing by 1.38%/million years, we estimate the divergence of Yemeni and Somali *Pelomedusa* to be ~2.4 mya. This date is nested within the divergence date estimate from BEAST.

3. DISCUSSION

Our sampling for this study is by no means complete, as *Pelomedusa* is found throughout sub-Saharan Africa. Relative to other animal groups, turtles are relatively under-collected since their secretive lifestyle makes them difficult to capture and their large size makes them difficult to transport. However, we have compiled all known, available samples for this study and use this opportunity to provide preliminary phylogeographic data on this understudied taxon. Our phylogenetic analyses put the sister relationship of *Pelusios* and *Pelomedusa* into question. *Pelusios* was either nested within *Pelomedusa* or placed in a polytomy with two *Pelomedusa* clades. These results could have several explanations: 1) an artifact of the markers we have used (i.e., incomplete lineage sorting), 2) a rapid radiation early in the history of the family Pelomedusidae, resulting in a hard polytomy, or 3) *Pelusios* diverging from within *Pelomedusa*. This result does not seem to be an artifact of the markers used, as Vargas-Ramirez et al. (2010) found similar results with different markers. Therefore, the relationship between *Pelusios* and *Pelomedusa* appears to be more complicated than previous believed and should be further studied.

Divergence date estimates from both the BEAST and the molecular rate of evolution analyses are concordant, as the point estimate is nested within the BEAST range. Despite the uncertainty in the wide range from BEAST, these analyses provide valuable insight, and are incorporated into the discussion below.

3.1 The Western Clade: The Sahel and the Savanna

Pelomedusa samples in the Western clade do not always show close affinity to geographic neighbors; although the Nigerian sample is only ~200km from the Cameroon sample, Nigeria is more closely related to samples ~1000km away in Senegal. Instead of geography, the substructure of the Western clade seems to be based on ecoregion. The first group consists of individuals from Niger, Nigeria, and Senegal, and is found in the Sahel region of Africa. The Sahel region is just south of the Sahara Desert, and is a dry region that stretches across Africa from the Atlantic Ocean to the Red Sea (Fig. 2). The second group consists of individuals from Cameroon, Ghana, and Togo. These countries occur in the wetter savanna region to the south of the Sahel. This pattern is also seen in the lizard genus *Agama* (Leaché et al. 2009). The persistence of this biogeographic pattern between taxa suggests that there is relatively low interaction between the Sahel and savanna species.

3.2 The Eastern Clade: The Population in Yemen

Populations of *Pelomedusa* on the Arabian Peninsula are restricted to Yemen and Saudi Arabia (Boycott and Bourquin 2008). Due to the current political instability of the area, additional sampling from the area is difficult. With our current sampling we are able to gain insight into the relationship of the two populations, but this should be considered a working hypothesis until additional data are collected. As expected based on geography, the Yemeni specimen is most closely related to the population from neighboring Somalia.

Timing and geologic history must be considered when evaluating the mechanisms of isolated populations. These populations can naturally occur through vicariance or dispersal, or be a result of artificial, human transport. Although we can never definitively determine the cause of a disjunct population, analyzing geologic and molecular data can help us evaluate the likelihood of a particular event occurring.

In all phylogenetic analyses, the individual from Yemen is the sister to the Somalia clade, and is different by an uncorrected pair-wise difference of ~6%. Our divergence dating analyses estimate a date of 14.1-1 mya (BEAST) or 2.4 mya (molecular rate of evolution) for the minimum divergence time. Although there is a wide range in dates, these data indicate that the event was relatively old, most likely before the Pleistocene. These data indicate that *Pelomedusa* populations on the Arabian Peninsula are most likely naturally occurring, and not a result of human introduction.

If not anthropogenic, then we can consider natural mechanisms of vicariance or dispersal to explain this biogeographic pattern. Based on the *Pelusios* fossil from our divergence dating analyses, we estimate the age of *Pelomedusa* to be 23.6-13.9 mya. Based on this estimate, the formation of the Red Sea 26-25 mya (Gass 1977) predates the divergence of the family *Pelomedusa*, making a vicariance event highly unlikely.

The remaining possible mechanisms of *Pelomedusa* on the Arabian Peninsula involve a dispersal event, either over land or water. The African-Arabian distribution is not unique to *Pelomedusa*. This geographic pattern is also seen in hamadryas baboons (*Papio*; Winney et al. 2004), snakes (*Naja* [Trape et al. 2009], *Echis* [Pook et al. 2009], *Coluber* [Leviton 1986]), spiny-tailed lizards (*Uromastyx*; Amer and Kumazawa 2005), and skinks (*Chalcides*; Greenbaum et al. 2006). In each of these taxa, dispersal over land bridges has been hypothesized either via a northerly route through Egypt and the Sinai peninsula (*Uromastyx*, *Echis*), or via a southerly route (*Papio*, *Chalcides*) across a land bridge over the Strait of Bab el Mandeb. The hypothesis that a population could have dispersed around the Sinai Peninsula is less plausible in *Pelomedusa* because its current range does not extend up to the Red Sea's northern coast (Boycott and Bourquin 2008), and there is no fossil evidence to suggest that the historic range of *Pelomedusa* ever spanned that region (Wood 1973). In the southern end of the Red Sea, Africa and Arabia were intermittently connected and disconnected during subsequent movement of the Arabian and African plates. Although the geology of the Red Sea and the timing of land bridges are still controversial (Leviton 1986; Rohling et al. 1998; Siddall et al. 2003; Fernandes et al. 2006), our divergence dates infer that the establishment of *Pelomedusa* on the Arabian Peninsula was before the Pleistocene, making it unnecessary to consider Pleistocene fluctuations in sea level (Rohling et al. 1998; Siddall et al. 2003). However, Fernandes et al. (2006) estimate the presence of a land bridge between 12-6 mya, which cannot be discounted for *Pelomedusa*.

A natural over-water dispersal was not considered for other African-Arabian distributed taxa since the Red Sea is a likely barrier to dispersal for non-aquatic species. For the aquatic *Pelomedusa*, additional possibilities of rafting or swimming across the Red Sea are possible, as some freshwater turtles have been shown to be surprisingly salt tolerant (Dunson and Moll 1980; Dunson and Seidel 1986). Lower sea levels in the past, shortening the over-water distance between Somalia and Yemen, would make these scenarios even more plausible.

Our data suggest that the Arabian population of *Pelomedusa* is not the result of either an anthropogenic or vicariance event, but rather a pre-Pleistocene, naturally occurring dispersal event over a land bridge or water in the southern end of the Red Sea. Further sampling around the Red Sea coupled with refined geologic data may help us resolve the biogeographic history of *Pelomedusa* on the Arabian Peninsula.

3.3 The Southern Clade: The Population in Madagascar

The population in Madagascar is most closely related to the specimens from Malawi and Namibia, its nearest geographic neighbors included in this study. Similar to the analysis for the Eastern clade, both timing and geology of the region need to be considered to evaluate the cause of the disjunct population in Madagascar.

There are two traditional hypotheses to account for naturally occurring populations in Madagascar: continental drift vicariance and over water dispersal. The continental drift vicariance hypothesis requires that the population in Madagascar was already established at least 165 million years ago (Rabinowitz et al. 1983), before the split from the main Gondwana land mass. This seems an impossible scenario because the breakup of Madagascar from mainland Africa predates the origin of the genus *Pelomedusa* by more than 130 million years.

The over water dispersal hypothesis relaxes the time frame by allowing a dispersal to happen any time after 165 mya. Although Raxworthy (2003) puts *Pelomedusa* on a short list of species that "may represent natural yet (in evolutionary time scales) recent immigrant species", this seems unlikely considering the *Pelomedusa's* life history; *Pelomedusa* is a bottom walker rather than a swimmer, and prefers very little current in the water (Raxworthy 2003). The strong currents (e.g. Siddall et al. 2003) and width of the Mozambique Channel make the scenario of a natural, over-water dispersal event less likely.

Divergence dating analyses estimates do not provide much insight on the dating of this event (10.1– 0.0006 mya). However, phylogenetic analyses show that the individual from Madagascar is genetically very similar to the rest of the southern clade (uncorrected pair-wise difference

0.3–1.5%), despite the long geographic distance (800–1600km). The relatively low sequence divergence across such a large distance points towards a recent split between the lineages in southern Africa and Madagascar. Therefore, we believe the Malagasy population is most likely the result of a recent, human-mediated introduction. Additional sampling in southern Africa and Madagascar, focusing on genetic diversity and relationships between geographic areas, may help to resolve this issue.

5. Conclusion

Our preliminary phylogeographic study reveals considerable diversity and genetic structure within *Pelomedusa subrufa*, currently recognized as a single species. Phylogeographic patterns of mainland African *Pelomedusa* mirror that found in another pan-African reptile (Leaché et al. 2009). Based on geologic and molecular data, the disjunct populations of *Pelomedusa* on the Arabian Peninsula and Madagascar seem to have different histories, with the former being an old dispersal event, while the latter seems to be a recent human introduction. The major conclusions of our study are corroborated by Vargas-Ramirez et al. (2010), a concurrent study that was undertaken in an independent laboratory that we were made aware of during the publishing of our study.

Since we were unable to obtain dense sampling across *Pelomedusa's* range, our work should be seen as preliminary. Data presented in this study provides a framework to direct future genetic surveys. There is a need to further explore the *Pelomedusa subrufa* populations across the natural water ways and populations in the hypothesized contact zones between the three subclades. Denser sampling through these key areas could further illuminate the genetic complexity within this pan-African turtle, and ultimately offer key insight into the biogeographical phenomenon across Africa.

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Appendix I

Flanking primers used to amplify and sequence molecular markers in this study.

Gene	Primer Pair	Reference
12S	N/12SA, P/12SB	Palumbi et al. 1991
16S	M89(L), M90(H)	Georges et al. 1999
CytB	Bcytb, L	Palumbi et al. 1991; Shaffer et al. 1997
CO1	M72(L), M73(H)	Georges et al. 1998
R35	R35ex1, R35ex2	Fujita et al. 2004

Appendix II

Internal primers specific to Pelomedusa used to amplify and sequence molecular markers in this study.

Gene	Primer	Sequence (5' -> 3')	Primer Pair
16S	16S.L	TAAGACGAGAAGACCCTGTG	M90(H)
	16S.H	GCTGTTATCCCTGGGGTA	M89(L)
CytB	Cytb.R2	CGGGTTARGGTWGSRTTGTC	Bcytb
	Cytb.F1	CCTWCCATGAGGMCAAATATC	Cytb.R1
	Cytb.R1	GKRTGAARTTYTCWGGGTCTG	Cytb.F1
	Cytb.F2	GGATCHAACAAYCCMACAGGACT	L
CO1	CO1.H	GGCTCATARTATWGGRGCTTC	M72(L)
R35	R35.R3	AGTTAACCTAATGCCTGCC	R35ex1
	R35.F1	TCCAGTTTTACATCAGTGTAACTC	R35.R2
	R35.R2	AGAATGACACTGAACAATTCC	R35.F1
	R35.F2	TGTGTAATGTATGGAAAGGATAA	R35.R1
	R35.R1	GTGACTTTGACAGATGCTAGAA	R35.F2
	R35.F3	GAAACCCAGTCTTGCCTT	R35ex2

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Phylogenetic Relationships Among Species of Southwest Asian Leaf-toed Geckos (*Asaccus*)

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The first molecular phylogenetic analysis of *Asaccus* reveals high sequence divergence among the sampled species. *Asaccus montanus* is recovered as the sister to all other species. Two Arabian species (*A. gallagheri, A. platyrhynchus*) form a monophyletic group as suggested earlier by morphological analyses. Our data show that *A. gallagheri* from Nizwa, Oman likely represents a new species. Samples of two species (*A. elisae, A. griseonotus*) from north of the Persian Gulf form a well-supported clade. The traditional concept of *A. elisae* likely represents more than one species, as the samples included here are paraphyletic with respect to *A. griseonotus*. The taxonomy of *A. elisae* awaits comparison with samples from the type locality in Iraq. Our inability to resolve the phylogenetic position of two species (*A. caudivolvulus* and *A. nasrullahi*) prevents testing biogeographic hypotheses involving the occurrence of *Asaccus* on either side of the Persian Gulf.

The gecko genus *Asaccus* Dixon and Anderson 1973 (Squamata: Gekkonidae) contains 10 currently recognized species of leaf-toed geckoes (Fig. 1). *Asaccus* are distributed in northeastern Arabia (Oman, U.A.E.) and the Zagros Mountains (Iran, Iraq) (Fig. 2). One widespread species extends into Turkey and Syria. Although species have been described from 1895 to 2009 (see Taxonomic History below, Fig. 3), the only previous phylogeny was based on morphological characters

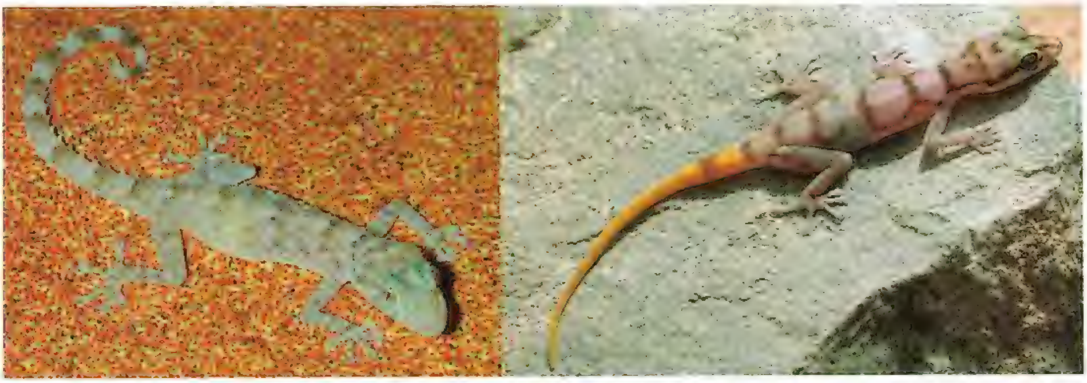

FIGURE 1. Left: *Asaccus montanus* from Nizwa, Oman (photo by TJP). Right: *Asaccus gallagheri* from Khasab, Oman. (photo by JFP).

(Arnold and Gardner 1994). Here we provide the first molecular phylogenetic analysis of the genus *Asaccus* using mitochondrial and nuclear DNA. This phylogeny provides insights into cryptic species diversity among Southwest Asian leaf-toed geckos and, by comparing our study with those on other taxa, contributes to the emerging biogeographic patterns for reptiles in the Persian Gulf region.

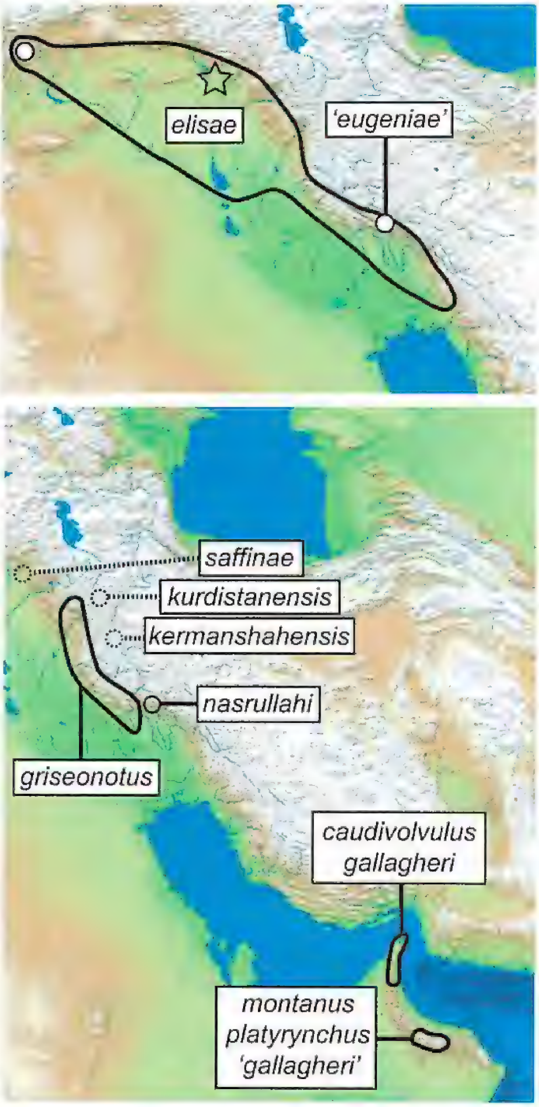

FIGURE 2. Map of samples used in this study. Top: The range of *Asaccus elisae*. The star indicates the type locality for the species in Iraq. The easternmost sample (circle) is from near the type locality of *eugeniae*, a species that may prove to be valid pending further study of the *A. elisae* complex. Bottom: Nine of the ten currently recognized species. *Asaccus* '*gallagheri*' from Oman is placed in quotes because of the high sequence divergence from topotypic specimens from the Musandam Peninsula. Circles indicate samples used in this study. Three Zagros endemics (*kermanshahensis*, *kurdistanensis*, *saffinae*) are shown with dashed lines indicating their absence from this study.

TAXONOMIC HISTORY

The first described Southwest Asian leaf-toed gecko was *Phyllodactylus elisae* Werner, 1895 from the ruins of the ancient city of Nineveh (near Mosul, Iraq). At that time, all leaf-toed geckos were placed in the widespread genus *Phyllodactylus*, a waste-basket taxon that included representatives from Asia, Africa, and the New World (see Bauer et al. 1997). Over a decade later, a second species was described from Dezful, Khuzestan Province, Iran (*Phyllodactylus eugeniae* Nikolskii, 1907). However, Werner (1917) synonymized *P. eugeniae* with *P. elisae*, which was accepted by subsequent authors (e.g., Wettstein, 1951; Wermuth, 1965). For several decades thereafter, the taxonomy of Southwest Asian leaf-toed geckos remained stagnant, with only one species, *P. elisae*, being recognized (Fig. 3).

The early 1970s brought a new cycle of research and discovery to Southwest Asian geckos in general, and leaf-toed geckos in particular. First, leaf-toed geckos were discovered on the Arabian Peninsula. *Phyllodactylus gallagheri* Arnold, 1972 was described from Masafi, Trucial States (now United Arab Emirates). The next year, Dixon and Anderson (1973) separated Southwest Asian leaf-toed geckos into a new genus, *Asaccus* (type species: *P. elisae*). About *P. gallagheri*, they stated, "Although we have not examined specimens of this new taxa [*sic*], we suspect that it is yet another representative of the genus *Asaccus* and would therefore extend the range of the genus southward onto the Arabian Peninsula" (Dixon and Anderson, 1973:157). In that paper they also described a third species of *Asaccus*, *A. griseonotus*, from Iraq and Iran. Around the same time, Eiselt (1973) described *Asaccus ingae* from Lorestan Province, Iran. This species has been regarded as a junior synonym of *A. griseonotus* (Anderson, 1999:136) based on the month of description (December 1973 versus November 1973).

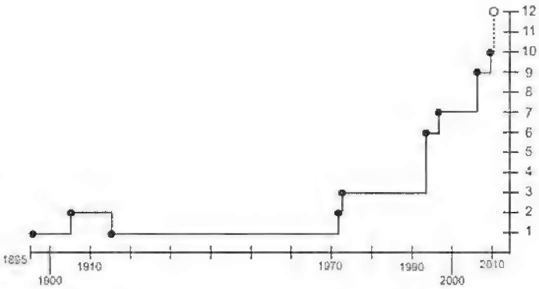

FIGURE 3. Number of species of *Asaccus* recognized through time. Dashed line and hollow circle show the postulated number of species based on the phylogeny and sequence divergence found in this study.

In 1977, Arnold reported the first records of *A. elisae* from the Arabian Peninsula from localities in the eastern United Arab Emirates and Oman, including the Musandam Peninsula of northern Oman and the Al Hajar Mountains nearly 300 kilometers southeast of the Musandam. Arnold (1977) noted extensive morphological variation among the samples of Arabian *A. elisae*, but postponed describing new species until specimens from the intervening 300 km could be examined. He later reiterated the distinctiveness of the Arabian samples, "Arabian populations of *Asaccus elisae* sen. lat. occur in two separate areas, each of which has distinct morphological characters. Both differ markedly from animals in Iraq and Iran and deserve at least subspecies status" (Arnold 1986:418). Arnold and Gardner (1994) later described these populations as *A. platyrhynchus* (Jebel Akhdar, Oman) and *A. caudivolvulus* (Musandam Peninsula region of U.A.E. and Oman). In the same year, Gardner (1994) reported a completely new species, *A. montanus*, from the Saiq Plateau of the Jebel Akhdar. Shortly thereafter, Rastegar-Pouyani (1996) described a new species from Iran *Asaccus kermanshahensis*, bringing the recognized species of *Asaccus* from three to seven between 1994 and 1996.

In just the past few years, three additional species have been described from Iran and Iraq: 1) *Asaccus nasrullahi* Werner, 2006 from the central Zagros Mountains of Lorestan Province, Iran (based on the reexamination of a specimen that was originally identified as *Ptyodactylus hasselquistii* by Schmidt [1955]); 2) *Asaccus kurdistanensis* Rastegar-Pouyani, Nilson, and Faizi, 2006 from the Zagros Mountains in the Sarvabad region of Kurdistan Province, Iran; and 3) *Asaccus saffinae* Afrasiab and Mohamad, 2009 from a cave in the Irbil region of Iraqi Kurdistan.

To summarize, the diversity of the Southwest Asian leaf-toed geckos (now all referred to genus *Asaccus*) has been unfolding over the past century, although for most of this time, 1895-1972, only a single species was considered valid (Fig. 3). Given that molecular phylogenetics can often reveal hidden evolutionary lineages (e.g., Stuart et al. 2006; Parham and Papenfuss 2009), we expect that such studies, combined with traditional morphological analyses and fieldwork, will result in the recognition of even greater species diversity within this clade.

MATERIALS AND METHODS

Our study includes DNA sequence data from 12 museum vouchers at the California Academy of Sciences, San Francisco, California, USA (CAS) and the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA (MVZ). Detailed locality information is available from these institutions. Species names, general localities, museum tissue and voucher numbers and GenBank numbers are presented in Table 1. Our samples represent seven of the 10 currently recognized species of *Asaccus*, lacking three species from Iran and Iraq (*A. kermanshahensis*, *A. kurdistanensis*, *A. saffinae*). Species names for the populations sampled were selected using the following criteria: (1) specimens that match the original morphological descriptions and were collected from localities given for holotype or paratypes (*A. caudivolvulus*, *A. griseonotus*, *A. montanus*,

TABLE 1. Samples of *Asaccus* and *Haemodracon* sequenced in this study.

Species	General Locality	Voucher number	Tissue Number	Genbank RAG-1	Genbank ND2
H. riebeckii	Socotra Island	MVZ 236486	MVZ 236486	HM212506	HM212518
A. caudivolvulus	Khasab, Oman	CAS 225372	MVZ 241367	HM212507	HM212519
A. elisae	Sanliurfa, Turkey	CAS 218142	CAS 218142	HM212509	HM212521
A. elisae	Sanliurfa, Turkey	CAS 218143	CAS 218143	HM212510	HM212522
A. elisae "eugeniae"	Khuzestan, Iran	MVZ 234315	MVZ 234315	HM212511	HM212523
A. gallagheri	Khasab, Oman	CAS 225358	MVZ 241368	HM212513	HM212525
A. gallagheri	Nizwa, Oman	CAS 225379	MVZ 241371	HM212516	HM212528
A. griseonotus	Lorestan, Iran	MVZ 234325	MVZ 234325	HM212512	HM212524
A. griseonotus	Lorestan, Iran	MVZ 234326	MVZ 234326	HM212508	HM212520
A. montanus	Nizwa, Oman	CAS 225399	MVZ 241370	HM212515	HM212527
A. nasrullahi	Khuzestan, Iran	MVZ 234330	MVZ 234330	HM212514	HM212526
A. platyrhynchus	Nizwa, Oman	CAS 225386	MVZ 241372	HM212517	HM212529

A. platyrhynchus, *A. nasrullahi*) or (2) specimens identified using keys in Arnold and Gardner (1994) and collected from localities within the known range of a given species (*A. gallagheri*; *A. elisae*). The outgroup, *Haemodracon riebeckii* (Peters, 1882), from Socotra Island, is strongly supported to be sister to *Asaccus* within the Phyllodactylidae (Gamble et al. 2008).

Total genomic DNA was extracted from liver or muscle tissue using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.). A fragment of mitochondrial DNA that encodes the complete NADH dehydrogenase subunit 2 gene and flanking tRNAs (simply 'ND2' hereafter) was amplified by the polymerase chain reaction (PCR; 94°C 45s, 48°C 30s, 72°C 1 min) for 35 cycles using the primer L4437 (Macey et al., 1997) and H5934 (Macey et al., 1997) or H-Alaliz (5'-AAAGTGTTTGAGTTGCATTCA-3'). A fragment of nuclear DNA that encodes part of the recombination activating protein 1 (RAG-1) gene was amplified by PCR (94°C 45s, 55°C 30s, 72°C 1 min) for 35 cycles using the primers L-RAG1b and H-RAG1b (Kearney and Stuart, 2004). PCR products were electrophoresed in a 1% low melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double strand cycle sequencing using the amplifying primers and Big Dye version 3 chemistry (Perkin Elmer). The internal primers L-snRAG1 and H-snRAG1 (Kearney and Stuart, 2004) were also used in the RAG-1 sequencing reactions. Cycle sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a Prism 3100 Genetic Analyzer (ABI) or 3730 DNA Analyzer (ABI). Sequences were edited using Sequencher v. 4.1 (Genecodes). Sequences were aligned using Geneious Pro 4.6 software (Biomatters, Auckland, New Zealand) and adjusted by eye. Phylogenetic relationships among the samples were assessed using Maximum Likelihood. The Akaike Information Criterion (AIC) in ModelTest 3.06 (Posada and Crandall, 1998) was used to find the model of evolution that best fit the data. The GTR + Γ + I model was used in GARLI 0.951 (Zwickl 2006) with simultaneous tree and parameter estimations. We used nonparametric bootstraps (1000 pseudoreplicates) to assess node support in resulting topologies.

RESULTS

A 1287 bp fragment of mtDNA (ND2) and a 1381 bp fragment of nuclear DNA (RAG-1) were obtained from all samples. The mitochondrial sequence divergence among species of *Asaccus* (Table 2) is extremely high (over 39% HKY corrected sequence divergence for ND2) and nearing saturation (see Discussion). The resultant phylogenetic trees are shown in Figs. 4B–D. Although RAG-1 is far less variable than ND2 (Table 2), the combined tree topology is the same as the RAG-1 topology (Fig. 4D), suggesting that the small number of informative sites contains far less noise than ND2. Increasing the length of RAG-1 sequences should improve support for branches in the combined tree. The only difference between the ND2 and RAG-1 tree is the placement of *A. nasrullahi*, which receives weak support as the sister to *A. caudivolvulus* in the ND2 tree (Fig. 4B) and is sister to all *Asaccus* except *A. montanus* in the RAG1 tree (Fig. 4C). Aside from the relationships of *A. nasrullahi*, all taxon clusterings within *Asaccus* receive high bootstrap values in the combined tree. In contrast to the previous phylogenetic hypothesis of *Asaccus* relationships (Arnold and Gardner 1994; Fig. 4A), our study recovered *A. montanus* as the sister to all other sampled species (Fig. 4B–D). Two Arabian species (*A. gallagheri* and *A. platyrhynchus*) form a monophyletic group as hypothesized by Arnold and Gardner (1994: Fig. 4A) on morphological characters (a caudal tubercle and sexually dimorphic tail color).

DISCUSSION

The high sequence divergence between species of *Asaccus* (Tables 2, 3) suggests that it is a very old clade. The HKY corrected sequence divergence between *Asaccus* and its sister taxon *Haemodracon* Bauer, Good, and Branch, 1997 is 31.3-37.6% (Table 2). Such high sequence divergence is nearly comparable to that among species of the sphaerodactylid gekko genus *Pristurus* Rüppell, 1835 (up to 42.4% in 'ND2', Papenfuss et al. 2009) which shares a distribution with the *Haemodracon* + *Asaccus* clade, occurring in both Oman and the island of Socotra. These high divergences certainly reflect saturation of the ND2 gene. Uncorrected distances between squamates and birds are 41.5% for the ND2 gene, indicating that 40% represents an approximate upper ceiling on meaningful distances for ND2.

Zoogeographically, *Asaccus* is one of several taxa that have closely related populations or species distributed on either side of the Persian Gulf (Arnold 1972). Rastegar-Pouyani et al. (2006) hypothesized that the Zagros was the center of origin of *Asaccus*, but our data show that *A. montanus* from Arabia is the most basal species. Unfortunately, further discussion of the biogeography of *Asaccus* across the Persian Gulf must await analysis of the three Zagros endemics (*A. kermanshahensis*, *A. kurdistanensis*, *A. saffinae*), and resolving the uncertain phylogenetic position of *Asaccus caudivolvulus* and *A. nasrullahi*.

In a few cases, our data indicate that current taxonomy is underestimating total diversity of *Asaccus*. The ND2 sequence divergence is very high (14.0%, Table 2) between the two samples of *A. gallagheri* from Nizwa and Khasab (Oman) implying that more than one species is present. Since our sample from Khasab is near to the type locality in the U.A.E., the divergent sample from Nizwa may represent a new species. Additional morphological study and fieldwork for geographically intervening samples are needed to delineate species boundaries for the putative taxa within *A. gallagheri*. Mitochondrial data also show that our Iranian sample of *A. elisae* is more closely related to *A. griseonotus* than it is to the Turkish samples of *A. elisae*. Clearly the concept of *A. elisae* represents more than one species. The Iranian sample is from near the type locality of *Phyllodactylus eugeniae*, which is currently in the synonymy of *A. elisae* (see Taxonomic History sec-

TABLE 2. HKY corrected distances for ND2 above the diagonal and uncorrected distances below.

	1	2	3	4	5	6	7	8	9	10	11	12
1 *Asaccus caudivolvulus* MVZ241367	—	0.32663	0.32663	0.35698	0.34578	0.39492	0.33187	0.33471	0.39084	0.32313	0.41360	0.44215
2 *Asaccus elisae* CAS218142	0.25789	—	0.00000	0.18116	0.34621	0.37899	0.17312	0.17215	0.34132	0.31061	0.39655	0.42052
3 *Asaccus elisae* CAS218143	0.25789	0.00000	—	0.18116	0.34621	0.37899	0.17312	0.17215	0.34132	0.31061	0.39655	0.42052
4 *Asaccus elisae "eugeniae"* MVZ234315	0.27601	0.15678	0.15678	—	0.27161	0.29328	0.15012	0.15629	0.39083	0.33245	0.43670	0.44991
5 *Asaccus gallagheri* MVZ241368	0.27186	0.27207	0.27207	0.27981	—	0.16018	0.35908	0.36320	0.42212	0.36503	0.35637	0.49132
6 *Asaccus gallagheri* MVZ241371	0.29881	0.28973	0.28973	0.29328	0.13977	—	0.39690	0.39822	0.46805	0.39674	0.37367	0.52984
7 *Asaccus griseonotus* MVZ234325	0.26178	0.15085	0.15085	0.13186	0.35908	0.39690	—	0.00637	0.37779	0.31367	0.40134	0.41463
8 *Asaccus griseonotus* MVZ234326	0.26366	0.15014	0.15014	0.13646	0.28213	0.30004	0.00633	—	0.38402	0.32270	0.40485	0.42434
9 *Asaccus montanus* MVZ241370	0.29922	0.26984	0.26984	0.29983	0.31601	0.33991	0.29109	0.29471	—	0.39185	0.49501	0.43831
10 *Asaccus nasrullahi* MVZ234330	0.25725	0.25085	0.25085	0.26434	0.28361	0.30141	0.25236	0.25780	0.29812	—	0.43297	0.42806
11 *Asaccus platyrhynchus* MVZ241372	0.30945	0.30027	0.30027	0.32287	0.27801	0.28717	0.30301	0.30542	0.35251	0.32251	—	0.53895
12 *Haemodracon riebeckii* MVZ236486	0.32834	0.31581	0.31581	0.33183	0.35453	0.37116	0.31318	0.31856	0.32444	0.32027	0.37607	—

TABLE 3. HKY corrected distances for RAG-1 above the diagonal and uncorrected distances below.

	1	2	3	4	5	6	7	8	9	10	11	12
1 *Asaccus caudivolvulus* MVZ241367	—	0.01469	0.01617	0.01319	0.01546	0.01469	0.01467	0.01501	0.02139	0.01916	0.01394	0.04597
2 *Asaccus elisae* CAS218142	0.01452	—	0.00073	0.00146	0.01845	0.01767	0.00291	0.00235	0.02515	0.01765	0.01617	0.05239
3 *Asaccus elisae* CAS218143	0.01595	0.00073	—	0.00291	0.01991	0.01914	0.00436	0.00391	0.02665	0.01913	0.01764	0.05481
4 *Asaccus elisae "eugeniae"* MVZ234315	0.01305	0.00145	0.00290	—	0.01691	0.01614	0.00145	0.00077	0.02361	0.01614	0.01540	0.05231
5 *Asaccus gallagheri* MVZ241368	0.01523	0.01814	0.01955	0.01665	—	0.00363	0.01690	0.01898	0.02516	0.02142	0.00729	0.05322
6 *Asaccus gallagheri* MVZ241371	0.01451	0.01741	0.01883	0.01593	0.00362	—	0.01614	0.01813	0.02513	0.02064	0.00582	0.05092
7 *Asaccus griseonotus* MVZ234325	0.01450	0.00290	0.00434	0.00145	0.01665	0.01593	—	0.00155	0.02511	0.01762	0.01539	0.05113
8 *Asaccus griseonotus* MVZ234326	0.01483	0.00234	0.00390	0.00077	0.01865	0.01786	0.00155	—	0.02461	0.01740	0.01655	0.05233
9 *Asaccus montanus* MVZ241370	0.02103	0.02465	0.02608	0.02317	0.02462	0.02462	0.02462	0.02414	—	0.02062	0.02438	0.05449
10 *Asaccus nasrullahi* MVZ234330	0.01885	0.01740	0.01884	0.01593	0.02100	0.02028	0.01738	0.01715	0.02028	—	0.01989	0.05207
11 *Asaccus platyrhynchus* MVZ241372	0.01378	0.01596	0.01738	0.01521	0.00724	0.00579	0.01521	0.01632	0.02390	0.01955	—	0.05085
12 *Haemodracon riebeckii* MVZ236486	0.04442	0.05039	0.05260	0.05031	0.05108	0.04897	0.04922	0.05033	0.05233	0.05002	0.04894	—

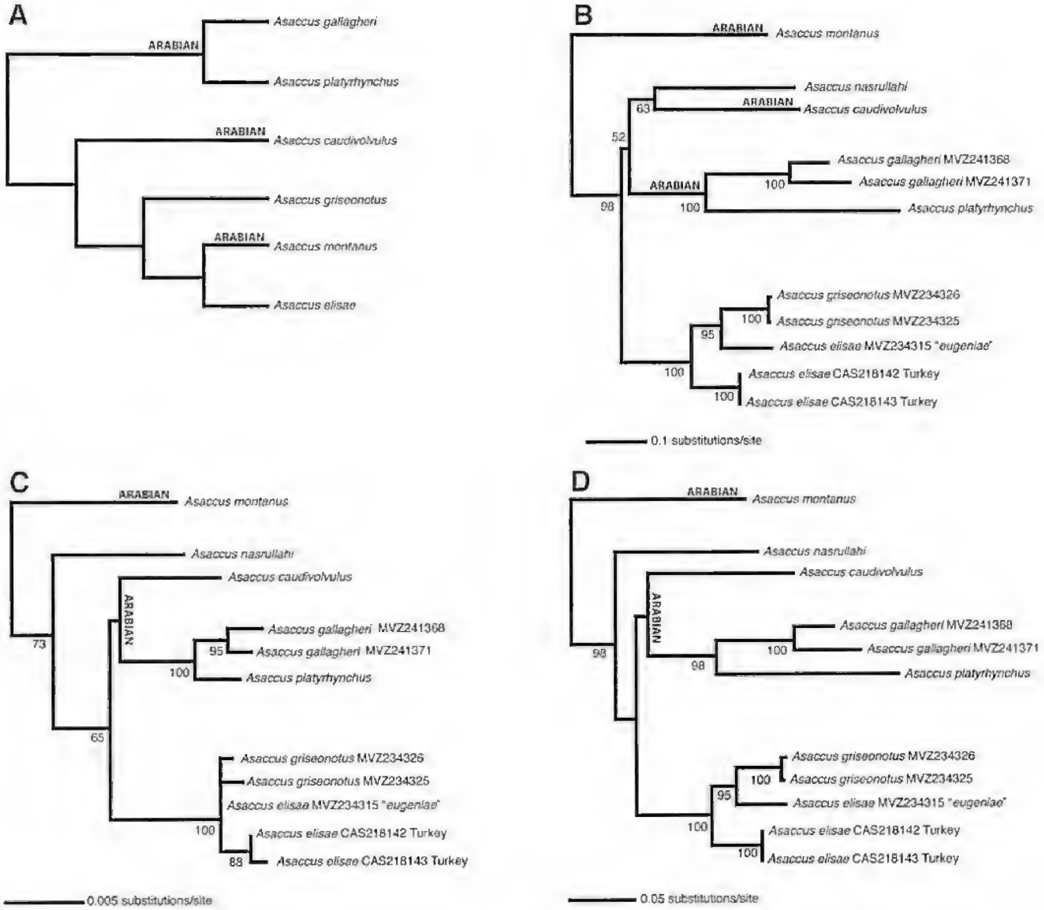
A
ARABIAN
Asaccus gallagheri
Asaccus platyrhynchus
ARABIAN
Asaccus caudivolvulus
Asaccus griseonotus
ARABIAN
Asaccus montanus
Asaccus elisae
B
ARABIAN
Asaccus montanus
Asaccus nasrullahi
ARABIAN
Asaccus caudivolvulus
63
52
Asaccus gallagheri MVZ241368
Asaccus gallagheri MVZ241371
ARABIAN
100
Asaccus platyrhynchus
98
100
Asaccus griseonotus MVZ234326
100
Asaccus griseonotus MVZ234325
95
Asaccus elisae MVZ234315 "eugeniae"
100
Asaccus elisae CAS218142 Turkey
100
Asaccus elisae CAS218143 Turkey
0.1 substitutions/site
C
ARABIAN
Asaccus montanus
Asaccus nasrullahi
Asaccus caudivolvulus
ARABIAN
Asaccus gallagheri MVZ241368
95
Asaccus gallagheri MVZ241371
73
100
Asaccus platyrhynchus
65
Asaccus griseonotus MVZ234326
Asaccus griseonotus MVZ234325
Asaccus elisae MVZ234315 "eugeniae"
100
Asaccus elisae CAS218142 Turkey
88
Asaccus elisae CAS218143 Turkey
0.005 substitutions/site
D
ARABIAN
Asaccus montanus
Asaccus nasrullahi
Asaccus caudivolvulus
ARABIAN
Asaccus gallagheri MVZ241368
100
Asaccus gallagheri MVZ241371
98
98
Asaccus platyrhynchus
Asaccus griseonotus MVZ234326
100
Asaccus griseonotus MVZ234325
95
Asaccus elisae MVZ234315 "eugeniae"
100
Asaccus elisae CAS218142 Turkey
100
Asaccus elisae CAS218143 Turkey
0.05 substitutions/site

FIGURE 4. Phylogenetic hypotheses for the genus *Asaccus*. A: Phylogeny based on morphology (Arnold and Gardner, 1994); B-D: Maximum Likelihood analysis of mitochondrial DNA (ND2, B), nuclear DNA (RAG-1, C), and combined data (D).

tion above). Tok et al. (1997) and Baran et al. (2003) presented morphological data on *A. elisae* from Iraq, Iran, Syria, and Turkey and concluded that the observed variation was infraspecific. However, without examining or sequencing samples of topotypic *A. elisae* from Iraq it is difficult to know if the Iranian or Turkish samples studied here represent true *A. elisae* or should be referred to a new species. Likewise, although new populations of *Asaccus* continue to be discovered (Martens and Kock 1990; Franzen et al. 2002; Tok et al. 2002; Afrasiab and Mohamad 2009), our knowledge of the true distributional range of all members of the genus remains rudimentary and the geographic factors influencing species boundaries must remain speculative.

CONCLUSIONS

The first molecular phylogenetic analysis of *Asaccus* shows high sequence divergence among the sampled species. *Asaccus montanus* is revealed as the sister to all other species. Our inability to resolve the phylogenetic position of two species (*A. caudivolvulus* and *A. nasrullahi*) prevents the testing of biogeographic hypotheses involving the occurrence of *Asaccus* on either side of the Persian Gulf. Two Arabian species (*A. gallagheri*, *A. platyrhynchus*) form a monophyletic group as suggested by morphological analyses. Our data show that *A. gallagheri* from Nizwa, Oman likely represents a new species. Samples of two species (*A. elisae*, *A. griseonotus*) from north of the Persian Gulf form a well-supported monophyletic clade. The traditional concept of *A. elisae* likely represents more than one species, as the samples included here are paraphyletic with respect to *A. griseonotus*. The taxonomy of *A. elisae* awaits comparison with samples from the type locality in Iraq. In addition to the species descriptions outlined above, future directions include adding the missing Zagros endemics (*A. kurdistanensis*, *A. saffinae*) as well as sequencing additional markers in order to resolve the existing polytomies.

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The Flowering Plant Family Styracaceae in the Gaoligong Shan, along the Border Region of China and Myanmar

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A taxonomic revision of the flowering plant family Styracaceae in the Gaoligong Shan region of western Yunnan Province and extreme southeastern Xizang Province (Tibet) in China, and eastern Kachin State in northern Myanmar (Burma), is presented. Three genera are recognized from the region: *Huodendron* with three species, *Rehderodendron* with two species, and *Styrax* with two species. Both species of *Rehderodendron* are endemic to the Gaoligong Shan. The treatment includes a key to species, descriptions, specimen citations, and images or illustrations of some species. Also included are species distribution maps based on estimates of geographic coordinates of old collections and GPS-derived coordinates of more recent collections.

KEYWORDS: Burma, China, Styracaceae, Gaoligong Shan, Kachin, Myanmar, Taxonomy, Tibet, Yunnan, Xizang.

高黎貢山安息香科的分類修訂

本文對緬甸北部、雲南西部和西藏東南部的高黎貢山有花植物安息香科進行了分類修訂。本地區含三屬七種該科植物：山茉莉屬三種，木瓜紅屬兩種，安息香屬兩種。木瓜紅屬的兩種均為高黎貢山特有種。本修訂含分種檢索表，種的描述，文獻引證和部分種的野外照片和繪圖。同時具有來自類群新老標本資料的經緯度分佈圖

關鍵詞：緬甸，中國，安息香科，高黎貢山，克欽，分類學，西藏，雲南

As part of a long-term, large-scale multidisciplinary biotic survey and inventory of the Gaoligong Shan (GLGS), we continue to examine the taxonomy of several groups of vascular plants in this region for which we have expertise. The GLGS is a 600 km-long high-elevation mountain range that over much of its length straddles the border between China and Myanmar. It is situated at the heart of a vast biodiversity hotspot, i.e., a region of high numbers of species under severe threat of destruction through human activity (Li et al. 2000; Liu and Kress 2005; Stotz et al. 2003; Chaplin 2006). Our first two treatments of GLGS vascular plants, those of the Symplocaceae (Zhou et al. 2006) and *Gaultheria* (Fritsch et al. 2008), served as models for forthcoming treatments of other groups of interest to us. Here, we follow up these with a treatment for the flowering plant family Styracaceae.

The Styracaceae (order Ericales; Angiosperm Phylogeny Group III 2009), comprising 11 genera and about 160 species, are distributed throughout eastern Asia and much of the Americas. Its combination of tree or shrub habit, alternate, simple, estipulate leaves, stellate to peltate trichomes, generally cupuliform calyx, gamopetalous corolla, stamens adnate to the corolla, large anthers with massive connectives and longitudinally dehiscent thecae, and an ovary with distally attenuated septa continuing into the hollow (and thus fluted) style characterizes the family (Dickison 1993; Fritsch 2004). The Styracaceae are most diverse in eastern Asia. Ten of the 11 genera are present there, nine of which are endemic. Several Asian species of *Styrax* are economically important as the commercial sources of the balsamic resin benzoin, used in the pharmaceutical, confection, and fragrance industries (Duke 1985). Of the three genera of Styracaceae that occur in the GLGS, *Huodendron* and *Rehderodendron* are Asian endemics, whereas the large genus *Styrax* is found throughout the range of the family.

MATERIALS AND METHODS

The materials and methods generally follow those in Fritsch et al. (2008), with the following modifications. Approximately 150 collections (about 250 specimen sheets) of Styracaceae were studied from the GLGS and vicinity. The material examined comprises the Gaoligong Shan collections from KUN (the herbarium with the richest collection in SW China) and also those from A, AAU, BM, BO, CAS, E, GH, K, MO, and P. The collections of George Forrest are cited as "F"; the 14 collecting activities all with the same number series listed in Fritsch et al. (2008; Appendix 1) are cited as "GLGS." All descriptions are based on material exclusively from the GLGS. Leaf blade measurements are from the larger leaves on each specimen. Leaf blade color was assessed in the dry state. Calyx dimensions are presented as height (from the end of the pedicel to the distal margin) times width at the apex, and thus include the short hypanthium. The dimensions of the fruiting calyx in *Styrax* (the calyx is persistent) are presented as separate from those of the fruit proper. Fruit measurements exclude the apical rostrum. For a map of Chinese counties (Xian) and Myanmar Districts included in the GLGS region cited in this work, see Zhou et al. (2006: Figure 3). The Chinese township (Xiang) from which specimens were collected are based on specimen labels when indicated, or estimated from maps in Zhao (2005). A list of species recognized, and an index to exsiccatae that we have examined for this study, are provided in Appendices 1 and 2, respectively.

TAXONOMIC TREATMENT OF STYRACACEAE

STYRACACEAE Dumortier, Anal. Fam. Pl. 28, 29. 1829. nom. cons.

Trees or shrubs, terrestrial, deciduous (GLGS), hermaphroditic (GLGS); indumentum of stellate trichomes (GLGS). Fertile shoots produced either laterally and (on at least some branchlets) terminally, or laterally only, on branchlets of previous growth period. Stipules absent. Leaves alternate (sometimes first two leaves opposite or subopposite), simple, petiolate; leaf blade venation of secondary veins pinnate. Inflorescences cymes, racemes, or panicles, or sometimes 1–2-flowered, bracteate (GLGS). Flowers actinomorphic, bracteolate, fragrant; hypanthium present, completely adnate to ovary wall. Calyx gamosepalous. Hypanthium + calyx generally obconical or cupuliform, ± 5-toothed or lobed (GLGS), with valvate or open aestivation. Corolla white (GLGS), sympetalous, tube not extending beyond adnation with androecium (GLGS), generally campanulate to open with lobes spreading to reflexed, stellate-pubescent (GLGS); lobes 5(–8), with imbricate or subinduplicate-valvate aestivation. Stamens generally twice the number of corolla lobes (GLGS), adnate to corolla; filaments flattened at least proximally, sometimes forming a tube proximally; anthers basifixed, introrse, 2-locular, longitudinally dehiscent, oblong to linear; connective large and tangentially thickened, sometimes surpassing thecae. Gynoecium 3- or 4-carpellate (GLGS); ovary partly to completely inferior, with essentially axile placentation, 3- or 4-septate proximally but 1-locular through distal attenuation of septa (GLGS); style 1, filiform, hollow (GLGS), fluted in line with ovary septa; stylodia completely connate or rarely distinct distally; stigma terminal, truncate, lobed, or capitellate; ovules ca. 4 or ca. 8–30 per carpel (GLGS), anatropous, unitegmic or bitegmic, tenuinucellate. Fruit dry (GLGS), either capsular with loculicidal dehiscence or indehiscent and longitudinally ribbed (GLGS); fruiting calyx persistent, epicarpous for various proportions of fruit length. Seeds 1– numerous, globose or ellipsoid to flattened-fusiform or cylindrical (GLGS), sometimes appendaged (GLGS); testa brown, thin to indurate; cotyledons flattened or nearly terete; endosperm copious, oily. $x = 8$ or 12.

Key to Genera of Styracaceae in the Gaoligong Shan

1a. Fertile shoots produced only laterally on branchlets of previous growth period; vegetative bud scales present; pedicels articulated; ovules 4 per carpel in two axial rows, upper 2 apotropous, lower 2 epitropous; fruit > 4 cm, indehiscent; fruiting calyx epicarpous the complete length of the fruit (excluding rostrum) . . . . 2. *Rehderodendron*
1b. Fertile shoots produced both laterally and (on at least some branchlets) terminally on branchlets of previous growth period; vegetative bud scales absent; pedicels not articulated; ovules ca. 8–30 per carpel, irregularly arranged; fruit < 2 cm, dehiscent; fruiting calyx epicarpous to ca. ⅔ the length of the fruit.
  2a. Anther connectives 2- or 3-dentate at apex; fruiting calyx epicarpous ⅓ to ⅔ the length of the fruit; seeds numerous, ≤ 3 mm, with a flat appendage on each end; seed coat thin. . . . . 1. *Huodendron*
  2b. Anther connectives not toothed at apex; fruiting calyx epicarpous only slightly beyond fruit base; seed 1(–3), > 6 mm, unappendaged; seed coat indurate . . . . 3. *Styrax*

1. **HUODENDRON** Rehder, J. Arnold Arbor. 16:341. 1935.

TYPE: *Huodendron tibeticum* (Anthony) Rehder.

山茉莉属 shan mo li shu.

Shrubs or trees, deciduous. Fertile shoots produced both laterally and (on at least some branchlets) terminally on branchlets of previous growth period; vegetative bud scales absent. First two leaves alternate; leaf blades chartaceous, margin entire or serrate. Inflorescences terminal or axillary, subcorymbose or paniculate. Pedicels not articulated. Calyx lobes 5, with valvate to open aestivation. Corolla divided nearly to base (i.e., petals coherent); lobes 5, with imbricate or subinduplicate-valvate aestivation, revolute. Stamens 8–10, subequal in length, adnate to very base of corolla, strongly exserted; tube absent; filaments pubescent; filament trichome branches circular in cross-section, glossy; anthers glabrous; connectives appendaged at apex, (2-)3-dentate. Carpels 3(4); ovary partly inferior; ovules numerous per carpel, irregularly arranged, unitegmic. Style divided ⅓–⅔ total length or if entire then stigma strongly lobed and capitellate. Some fruiting pedicels deflexed. Fruit capsular, loculicidally dehiscent, ovoid, to 7 mm; exocarp not ribbed; mesocarp absent; fruiting calyx epicarpous ⅓–⅔ the length of the fruit. Seeds numerous, ellipsoid or trigonous, appendaged on each end, to 3 mm; seed coat thin, reticulate.

A genus of 4 or 5 species distributed in China, Myanmar, Thailand, and Vietnam; 3 species in China, 0 endemic [Hwang and Grimes (1996)]; 1 species in Myanmar, 0 endemic [Kress et al. (2003)]; 3 species in the GLGS, 0 endemic.

All three species of *Huodendron* included in the treatments of Styracaceae for the *Flora Reipublicae Popularis Sinicae* (Hwang 1987) and *Flora of China* (Hwang and Grimes 1996) occur in the GLGS; our treatment comprises the same three species as those recognized in these treatments and in the *Flora of Gaoligong Mountain* (Li et al. 2000). No species of this genus was included in the *Flora Xizangica* (Flora of Tibet; Ming 1986), although the type of *H. tibeticum* (*G. Forrest 21648*) is from Tibet and our study includes several specimens of *H. tibeticum* from southeastern Tibet, within the GLGS. One species of *Huodendron* is recorded from Myanmar in Kress et al. (2003; *H. biaristatum*, cited as *Styrax biaristatus* W.W. Sm.).

The taxonomic status of *Huodendron siamense* Fletcher (Kew Bull. Misc. Inform. 1937:380. 1937. TYPE.— THAILAND. Ranawng, Kao Pawta Luang Keo, ca. 500 m, *F.G. Kerr 16909*, holotype: K), with only the type cited in the protologue, is unclear to us. We have seen no material of *Huodendron* from Thailand and know of no detailed floristic works that treat this name. The Latin diagnosis states that it has affinity to *H. biaristatum* but differs in its more numerous secondary leaf veins, prominent tertiary and quaternary veins above, and smaller flowers.

Huodendron yunnanense Hu (J. Roy. Hort. Soc. 63:388. 1938) is a *nomen nudum*.

Key to Species of *Huodendron* in the Gaoligong Shan

1a. Leaf blade midvein slightly raised or plane adaxially; inflorescence branches and pedicels glabrous; stamen filaments glabrous abaxially; style divided ⅓–⅔ total length, glabrous; fruit glabrous . . . . 2. *H. tibeticum*

1b. Leaf blade midvein sulcate adaxially; inflorescence branches and pedicels densely tomentose; stamen filaments tomentose abaxially; style divided near apex or entire, densely villous; fruit tomentose.

  2a. Leaf blades subcoriaceous, abaxially densely tomentose; inflorescences terminal . . . . 3. *H. tomentosum*

  2b. Leaf blades chartaceous, abaxially glabrous except often for tufted pubescence in axils of secondary veins, rarely sparsely tomentose; inflorescences terminal and axillary or both . . . . 1. *H. biaristatum*

1. Huodendron biaristatum (W.W. Smith) Rehder, J. Arnold Arbor. 16:344. 1935. Basionym: *Styrax biaristatus* W.W. Smith, Notes Roy. Bot. Gard. Edinburgh 12:233. 1920. TYPE.— CHINA. Yunnan: Tengchong Xian, Jietou Xiang, on the western flank of the Shweli-Salween divide, 25° 40′N, 9000 ft. [Gaoligong Shan], May 1919, *G. Forrest 18020* (lectotype, designated by Svengsuksa and Vidal 1992: P; isolectotype: E[2]!).

Huodendron chunianum Hu, Sunyatsenia 3(1):36–37, t. 7. 1935. (as *H.* "*Chunianum*") TYPE.— CHINA. Yunnan: Ping-pien Hsien, 1400 m, 16 May 1934, *H.T. Tsai 55091* (holotype: PE; isotype: A!).

Shrubs or trees to 18(–30) m tall. Young branchlets grayish green- or tawny tomentose basally, sparsely so or glabrous distally; vegetative buds densely grayish green- or tawny tomentose. Petiole 9–18 mm, glabrous or sparsely tomentose, occasionally densely so adaxially; leaf blade elliptic, elliptic-lanceolate, elliptic-oblong, or obovate-oblong, 9–18.7 × 2.1–4.8 cm, 3–5.6 times as long as wide, chartaceous, abaxially yellowish green or pale green, glabrous or rarely sparsely tomentose especially on midvein except for tufted-pubescent domatia often present at secondary vein axils, these often covered with a membranaceous flap of tissue, adaxially dark green, glabrous or sparsely tomentose on midvein, base cuneate, margin entire or serrulate with 1–ca. 20 teeth per side, often narrowly revolute, apex abruptly acuminate, midvein prominent abaxially, sulcate adaxially, secondary veins 4–9 per side, smaller veins tawny and raised abaxially, plane or slightly raised and tawny to dull orange adaxially. Inflorescences terminal or axillary or both, subcorymbose, 6–11 cm, 9- to ca. 60-flowered, rachis and branches densely grayish green-tomentose; pedicel 1–8 mm,

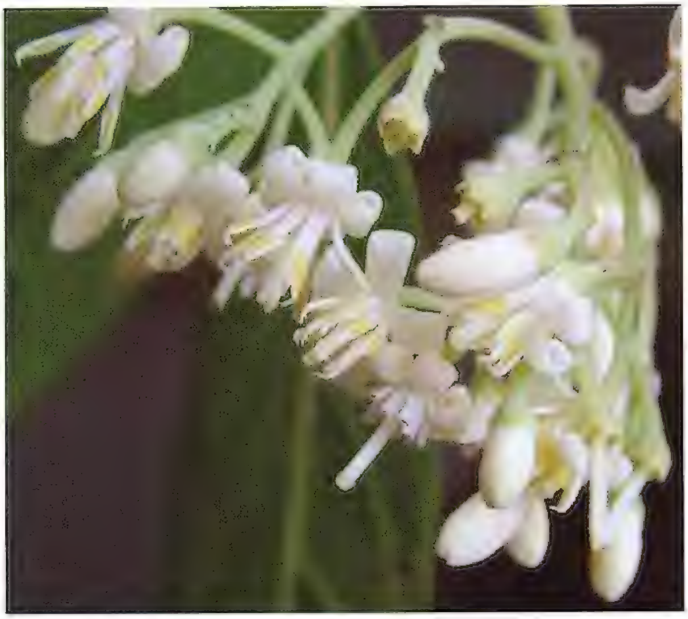


FIGURE 1. Inflorescence of *Huodendron biaristatum*. Note the stamens with apically toothed anther connectives. Photo by M. Dickson.

tomentose. Flowers 7–9 mm. Calyx 1.5–2 × 2.5–3.5 mm, densely grayish green-tomentose; calyx teeth broadly deltoid, 0.5–0.9 mm, densely grayish green-tomentose, sinus between the teeth concave. Corolla (and lobes) narrowly oblong, 6–9 × 1.7–2.8 mm, densely white-tomentose both sides. Stamen filaments 3–4 mm, densely tomentose both sides; anthers 3–4 mm, connective appendages 0.5–1.2 mm, (2)3-dentate at apex, teeth 0.2–0.6 mm, central tooth when present often shorter. Carpels 3; ovary densely tomentose. Style 5–8 mm, divided near apex or if entire then stigma strongly lobed, densely white-villous, becoming glabrous near apex. Fruit 4–7 mm, densely gray-tomentose. Seeds 1.3–3 mm, strongly flat-appendaged.

All GLGS material is *Huodendron biaristatum* var. *biaristatum*.

SELECTED ILLUSTRATIONS.— S.M. Hwang, Fl. Reipubl. Popularis Sin. 60(2):129 t. 43(6–12). 1987; B.K.K. Svengsuksa & J.E. Vidal, Fl. Cambodia, Laos, Viêtnam 26:191 t. 34 (7–13). 1992; C.Y. Wu & P.H. Raven, eds. Fl. China Ill. 15: t. 212(6–12). 2000.

PHOTOGRAPHIC IMAGE.— Figure 1.

PHENOLOGY.— Fl. May–Jun, fr. Aug–Dec.

DISTRIBUTION AND HABITAT.— Subtropical evergreen broadleaf forests, mixed forests, thickets, ravines; 1330–3000 m. In GLGS: CHINA. Yunnan: Fugong Xian (Lishadi Xiang), Gongshan Zizhixian (Dulongjiang Xiang), Longling Xian (Longjiang Xiang), Tengchong Xian (Jietou Xiang, Shangying Xiang, Wuhe Xiang); Figure 2. Outside of GLGS: Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Yunnan [Myanmar, Thailand, Vietnam].

CHINESE NAME.— 双齿山茉莉 shuang chi shan mo li

ADDITIONAL GAOLIGONG SHAN SPECIMENS EXAMINED: CHINA. YUNNAN: N'maika-Salween divide at Ho-lou, 7000–8000 ft., Aug 1919, *F 18400* (E); Nov 1919, *F 18833* (E). **FUGONG XIAN. Lishadi Xiang.** Mi'eluo Cun, near the Nujiang, E side of Gaoligong Shan, 1330 m, 17 Aug 2005, *GLGS 27688* (CAS). **GONGSHAN ZIZHIXIAN. Dulongjiang Xiang.** Between Shigong Qiao and Panjiasheng, trail from Bapo to Gongshan via Qiqi, W side of Gaoligong Shan, 2100–2200 m, 30 Oct 2004, *GLGS 21998* (CAS); above Panjiasheng between Shigong Qiao and Xixiaofang, trail from Bapo to Gongshan via Qiqi, W side of Gaoligong Shan, 2340 m, 2 Nov 2004, *GLGS 22102* (CAS). **LONGLING XIAN. Longjiang Xiang.**

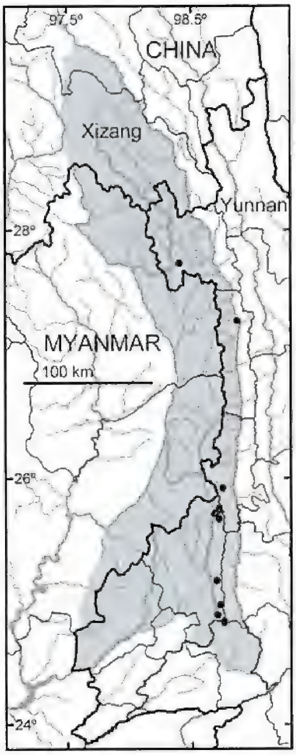


FIGURE 2. Distribution map of *Huodendron biaristatum* in the GLGS region.

Xiaoheishan Provincial Preserve, Xiaotai Shan, Xiaoshui He, W side of Gaoligong Shan, S of new rd from Baoshan to Tengchong via Nankang Yakou, 2011 m, 21 Aug 2003, *GLGS 17274* (CAS); vicinity of Xiaoheshan, along trail on S side of Hwy S317 (new hwy from Baoshan to Tengchong via Nankang Yakou) at km 23.5, W side of Gaoligong Shan, 2037 m, 23 May 2005, *GLGS 24631* (CAS); vicinity of Xiaoshuihe, Xiaoheishan Provincial Nature Reserve area, W side of Gaoligong Shan, 1990 m, 27 May 2005, *GLGS 25059* (CAS). **TENGCHONG XIAN. Jietou Xiang.** Shweli-Salween divide, 8000 ft., Jun 1916, *F 17894* (E); Shweli-Salween divide, 9000–10000 ft., Jun 1924, *F 24381* (E). Datang Cun, vicinity of Dongyanjiao, NNE of Datang, W side of Gaoligong Shan, 1930 m, 18 May 2006, *GLGS 30239* (CAS); Datang Cun, along Xiangshui He NNE of Datang, W side of Gaoligong Shan, 1900 m, 19 May 2006, *GLGS 30404* (CAS). **Qushi Xiang.** Shweli-Salween divide, 9000 ft., Dec 1924, *F 26108* (E). **Shangying Xiang.** Near Dahaoping, vicinity of km 50 on old rd from Baoshan to Tengchong, W side of Gaoligong Shan, 2050 m, 30 May 2005, *GLGS 25207* (CAS). **Wuhe Xiang.** Zhonglin, Jintang Village, W side of Gaoligong Shan, 1530 m, 24 May 2005, *GLGS 24819* (CAS).

2. Huodendron tibeticum (J. Anthony) Rehder, J. Arnold Arbor. 16:342. 1935. *Styrax tibeticus* J. Anthony, Notes Roy. Bot. Gard. Edinburgh 15:245. 1927. TYPE.— CHINA. Xizang: Zayü Xian, Tsarong Xiang, Salween-Kiu Chiang divide, NW of Si-chi-to, 28°35′N, 98°30′E, 10000–11000 ft., June 1922, *G. Forrest 21648* (holotype: E!).

Huodendron tibeticum (J. Anthony) Rehder var. *denticulatum* C.Y. Wu, Fl. Yunnan. 3:416. 1983. TYPE.— CHINA. Yunnan: Wenshan, Laojunshan, 1900 m, 19 May 1962, *K.M. Feng 22574* (holotype: KUN!).

Shrubs or trees to 30 m tall. Young branchlets grayish orange-tomentose basally, sparsely so or glabrous distally; vegetative buds densely grayish brown-tomentose. Petiole 5–11 mm, glabrous or sparsely tomentose, rarely more densely so adaxially; leaf blade oblong-elliptic or elliptic-lanceolate, 7.7–14.5 × 2.3–5.5 cm, 2.3–3.5 times as long as wide, chartaceous, abaxially yellowish green or pale green, glabrous except for tufted-pubescent domatia often present at secondary vein axils, adaxially green or dark green, glabrous or occasionally sparsely tomentose on midvein, margin entire or rarely very sparsely denticulate, often narrowly revolute, apex abruptly acuminate, midvein, secondary and tertiary veins tawny to dull orange, midvein raised abaxially, slightly raised or plane adaxially, secondary veins 5–9 per side, smaller veins raised on both sides, quaternary veins often green. Inflorescences terminal or axillary or both, subcorymbose, 3–6 cm, ca. 22- to 35-flowered, rachis base grayish orange-tomentose basally, otherwise rachis and branches glabrous; pedicel 2–6 mm, glabrous. Flowers 6–8 mm. Calyx 0.8–1.2 × 1.5–2.5 mm, glabrous; calyx teeth ovate-deltoid, 0.5–0.7 mm, glabrous except for white-ciliolate margins, sinus between the teeth ± notched. Corolla lobes linear-oblong, 5–6 × 0.8–1.3 mm, densely white-tomentose abaxially, less so adaxially to subglabrous. Stamen filaments 3–4 mm, glabrous abaxially, white-villous adaxially; anthers 2–2.6 mm, connective appendages 0.8–1 mm, 3-dentate at apex, teeth 0.3–0.7 mm, central tooth when present often shorter. Carpels 3; ovary glabrous. Style 6–7 mm, divided ⅓–⅔ total length, glabrous. Fruit 2.3–4 mm, glabrous. Seeds 0.8–1 mm, trigonous, weakly and irregularly appendaged.

The name *Huodendron tibeticum* var. *denticulatum* was not included in the treatment of Styracaceae for *Flora of China* (Hwang and Grimes 1996). This variety is reportedly distinguished from the nominate variety by its sparsely denticulate leaf margin, and eglandular-verrucose inflorescences, pedicels, and calices (Wu 1983). From examination of the type, we conclude that this variety falls well within the morphological variation seen in other specimens of *H. tibeticum* except for the presence of a single denticulation on one of the leaves, a difference that we consider to be taxonomically inconsequential.

SELECTED ILLUSTRATIONS.— S.M. Hwang, Fl. Reipubl. Popularis Sin. 60(2):129 t. 43(1–5).

1987; B.K.K. Svengsuksa & J.E. Vidal, Fl. Cambodia, Laos, Viêtnam 26:191 t. 34(1–6). 1992; C.Y. Wu & P.H. Raven, eds. Fl. China Ill. 15: t. 212(1–5). 2000.

Phenology.— Fl. Jun, fr. Aug–Jan.

Distribution and habitat.— Subtropical evergreen broadleaf forests, mixed forests, *Taiwania* forests, valleys, along rivers; 1300–3000 m. In GLGS: CHINA. Xizang: Zayü Xian (Tsarong Xiang). Yunnan: Fugong Xian (Lishadi Xiang, Lumadeng Xiang, Maji Xiang, Shangpa Zheng), Gongshan Zizhixian (Bingzhongluo Xiang, Cikai Zheng, Dulongjiang Xiang), Lushui Xian (Pianma Xiang); Figure 3. Outside of GLGS: NE Guangxi, Guizhou, W Hunan, SE Xizang, Yunnan [Vietnam].

Chinese name.— 西藏山茉莉 zi zang shan mo li

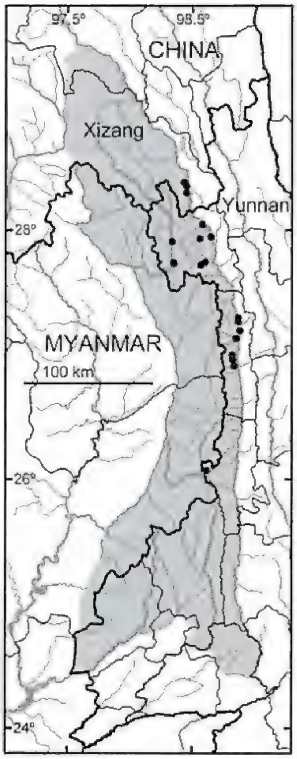


Figure 3. Distribution map of *Huodendron tibeticum* in the GLGS region.

Additional Gaoligong Shan specimens examined: CHINA. XIZANG: ZAYÜ XIAN. Tsarong Xiang. Salween-Kiukiang divide, W of Chamutoy, 11000–12000 ft., Oct 1922, *F 22882* (E); Mt. Kenichunpo, E and W slopes, Salwin and Irrawady divide, near banks of Salwin at Champutong, 7000 ft., May–Jul 1932, *J.F.C. Rock 22020* (E); Mt. Kenichunpo, mtns. W of Champutong, Upper Salwin River, 9000 ft., Oct 1932, *J.F.C. Rock 22474* (E). **YUNNAN:** 2000 m, 5 Jul 1978, *Bijiang Expedition 738* (KUN). **FUGONG XIAN. Lishadi Xiang.** Mi'eluo Cun, vicinity of Shiwanluo Village just above the Nujiang, E side of Gaoligong Shan, 1310 m, 12 Aug 2005, *GLGS 27335* (CAS); Ziguduo Cun, just S of Ziguduo Village near the Nujiang, E side of Gaoligong Shan, 1400 m, 13 Aug 2005, *GLGS 27469* (CAS). **Lumadeng Xiang.** Ca. 8 km from the Nujiang on rd to Yaping Pass, E side of Gaoligong Shan, ca. 25 direct km N of Fugong City, 1660 m, 25 Apr 2004, *GLGS 19467* (CAS). **Maji Xiang.** W side of the Nujiang, on opposite bank and SW of Wangjidu Village, E side of Gaoligong Shan, 1470 m, 20 Aug 2005, *GLGS 27924* (CAS). **Shangpa Zheng.** Qiao Mi Gu Lu, 2400 m, 8 Jun 1982, *Qinghai-Xizang Expedition 7106* (KUN); 2000 m, Oct 1934, *H.T. Tsai 59060* (KUN); 2000 m, 30 Oct 1934, *H.T. Tsai 59095* (KUN). **GONGSHAN ZIZHIXIAN. Bingzhongluo Xiang.** Sijitong, 2200–2500 m, 20 Sep 1940, *K.M. Feng 8024* (KUN); Ni Wa Di, 2000 m, 11 Oct 1956, *P.I. Mao 554* (KUN); Salwin Valley, SW of Champutong, 2200 m, 24 Jun 1938, *T.T. Yü 19154* (KUN). **Cikai Zheng.** E side of Gaoligong Shan, W of Gongshan, vicinity of Qiqi above the Pula He, 2000 m, 12 Jul 2000, *GLGS 12472* (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, along the Pula He, trail from Gazu to Qiqi and Dulongjiang Valley, 1800 m, 4 May 2002, *GLGS 14945* (CAS). **Dulongjiang Xiang.** Dulongjiang, E bank, commune #3, 1300 m, 26 Nov 1959, *K.M. Feng 24729* (KUN [2]); Xianjiudang, W side of Gaoligong Shan, along Dulongjiang Valley, trail from Kongdang to Dizhengdang, 1560 m, 23 Jul 2002, *GLGS 15221* (CAS); Qi Qi, 1900–2000 m, 18 Jul 1982, *Qinghai-Xizang Expedition 8125* (KUN); Qing Lang Dang, 1400 m, 12 Aug 1982, *Qinghai-Xizang Expedition 9249* (KUN). **LUSHUI XIAN. Pianma Xiang.** Hill behind Cixi, 2500 m, Jul 1964, *S.K. Wu 8293* (KUN).

3. Huodendron tomentosum Y.C. Tang ex S.M. Hwang, Acta Phytotax. Sin. 18:164. 1980. Type.— China. Yunnan: Ruili, 7 July 1938, *T.T. Yü 19219* (holotype: PE; isotype: A!).

Huodendron decorticatum C.Y. Wu, Fl. Yunnan. 3:418. 1983. Type.— China. Yunnan: Mar-li-po ["Malipo" in protologue], Hwang-jin-in, 1300–1600 m, 7 November 1947, *K.M. Feng 12999* [*"2999"* in protologue] (holotype: KUN!; isotype: A!).

Trees to 40 m tall. Young branchlets and vegetative buds densely grayish brown-tomentose. Petiole 9–20 mm, densely tomentose; leaf blade oblong, oblong-lanceolate, or oblong-oblanceolate, 8.5–12 × 2.9–4.2 cm, 2.5–3.4 times as long as wide, subcoriaceous, abaxially densely grayish green-tomentose, adaxially brownish green, glabrous, base cuneate, margin entire, often narrowly revolute, apex abruptly acuminate or rarely nearly acute; midvein prominent abaxially, slightly sulcate adaxially, other veins abaxially tawny, green to tawny orange adaxially, secondary veins 7–9 per side, secondary and tertiary veins sparsely tomentose or glabrous abaxially, quaternary veins obscured by tomentum abaxially. Inflorescences terminal, paniculate, 4–8 cm, ca. 50- to 60-flowered, rachis and branches densely grayish green-tomentose; pedicel 3–8 mm, tomentose. Flowers 7–8.5 mm. Calyx 1.5–2.5 × 2.5–3.5 mm, densely grayish green-tomentose; calyx teeth broadly deltoid, 0.3–0.7 mm, densely grayish green-tomentose, sinus between the teeth concave. Corolla lobes narrowly oblong, 5.5–6 × 1.7–2.2 mm, densely white-tomentose both sides. Stamen filaments ca. 3 mm, densely tomentose both sides; anthers 2.5–3 mm, connective appendages ca. 0.5 mm, 2- or 3-dentate at apex, teeth 0.2–0.4 mm, central tooth when present often shorter. Carpels 3 or 4; ovary densely grayish green-tomentose. Style 5.5–6.5 mm, divided near apex or if entire then stigma strongly lobed, densely white-villous. Fruit ca. 3 mm, densely grayish green-tomentose.

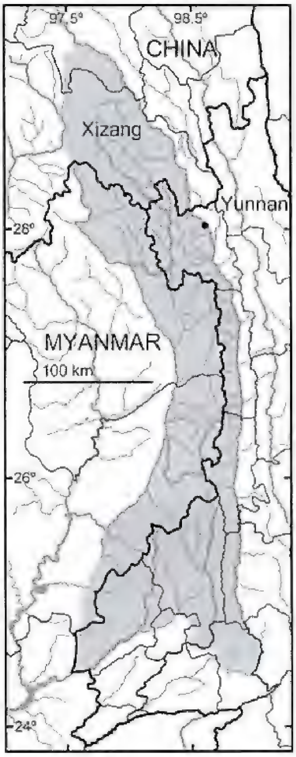


FIGURE 4. Distribution map of *Huodendron tomentosum* in the GLGS region.

Huodendron decorticatum C.Y. Wu (Wu 1983), described from a single collection from southeastern Yunnan, was included in neither the *Flora Reipublicae Popularis Sinicae* (Hwang 1987) nor the *Flora of China* (Hwang and Grimes 1996). In the original Latin diagnosis, this species was compared to *H. siamense* Fletcher (cited as *H.* "*siamicum*") from Thailand, having said to differ by leaves that are subcoriaceous, tomentose abaxially, and with an entire margin. The type material of this name does not appear to differ in any substantive way from that of *H. tomentosum* or the other material of *H. tomentosum* that we have seen. Thus we have placed *H. decorticatum* in synonymy under *H. tomentosum*. However, we do so with some hesitancy, because only a few collections of *H. tomentosum* have been made. More collections of this species would provide higher confidence for taxonomic assessment of these names.

The GLGS material is *Huodendron tomentosum* var. *tomentosum*.

SELECTED ILLUSTRATIONS.— S.M. Hwang, Fl. Reipubl. Popularis Sin. 60(2):129 t. 43(13–17). 1987; C.Y. Wu & P.H. Raven, eds. Fl. China Ill. 15: t. 212(13–17). 2000.

PHENOLOGY.— Young fr. Jun, mature fr. Nov.

DISTRIBUTION AND HABITAT.— 1600–1700 m. In GLGS: CHINA. Yunnan: Gongshan Zizhixian (Bingzhongluo Xiang); Figure 4. Outside of GLGS: N Guangxi, SW Yunnan [Vietnam].

CHINESE NAME.— 绒毛山茉莉 rong mao shan mo li

ADDITIONAL GAOLIGONG SHAN SPECIMEN EXAMINED: CHINA. YUNNAN: GONGSHAN ZIZHIXIAN. Bingzhongluo Xiang. 1600–1700 m, 4 Jul 1982, *Qinghai-Xizang Expedition 7949* (KUN).

2. REHDERODENDRON Hu, Sinensia 2:109. 1932.

TYPE: *Rehderodendron kweichowense* Hu, designated by Svengsuksa & Vidal,
Flore de Cambodge, du Laos, et du Viêtnam 26:182. 1992.

木瓜红属 mu gua hong shu.

Trees, deciduous. Fertile shoots produced only laterally on branchlets of previous growth period; vegetative bud scales present. First two leaves alternate; leaf blade margin serrate or entire. Inflorescences racemose or paniculate. Pedicels articulated. Hypanthium completely adnate to ovary. Calyx lobes 5, with open aestivation. Corolla lobes 5, with imbricate aestivation, basally short-connate, spreading. Stamens 10, 5 long and 5 short, adnate to ca. 1 mm beyond base of corolla; tube present or absent; filaments pubescent or glabrous; filament trichome branches (when present) flattened in cross-section, dull; anther connectives not surpassing thecae, not toothed, thecae glabrous. Carpels 3 or 4; ovary completely inferior; ovules 4 in two axial rows per carpel, upper 2 apotropous, lower 2 epitropous, unitegmic. Stylodia completely connate; stigma minutely lobed. Fruit woody, indehiscent, generally cylindrical, 5–7 cm (GLGS); exocarp ribbed; mesocarp indistinct from endocarp, internally lacunate; fruiting calyx epicarpous the complete length of the fruit (excluding the short rostrum). Seeds 1–3, narrowly cylindric; seed coat thin, fibrous.

A genus of ca. 6–8 species distributed in SW China, Myanmar, and Vietnam; ca. 6–8 species in China, 2–5 endemic; 0 species in Myanmar [Kress et al. (2003)]; 2 species in the GLGS, 2 endemic.

Of the five species of *Rehderodendron* recognized in Hwang and Grimes (1996), one is indicated as endemic to the GLGS (*R. gongshanense*), and two others are listed for large areas of Yunnan that could include the GLGS (*R. macrocarpum* and *R. kwangtungense*). The latter two species, however, do not occur in the GLGS according to a publication with detailed distributional information for Chinese vascular plants (Fu and Hong 2003). Neither Hwang (1987) nor Hwang and Grimes (1996) included three of the species of *Rehderodendron* from China that were published in *Flora Yunnanica* (Wu 1983). The distribution of two of these do not include the GLGS, but *R. microcarpum*, collected from within the GLGS and known only from the type at the time of publication, was recognized by Li et al. (2000; along with *R. gongshanense*) in the *Flora of Gaoligong Mountain*. From comparative examination of field and herbarium material of the types of *R. microcarpum* and *R. gongshanense*, as well as other specimens and images of *Rehderodendron* available to us, we agree with Li et al. (2000) in recognizing both of these species in the GLGS. They are both endemic to the GLGS. The distinctness of *R. gongshanense*, *R. kwangtungense*, and *R. macrocarpum* relative to one another, however, seems to merit further investigation and a detailed taxonomic field- and herbarium-based study of all species in the genus appears to be warranted.

Key to Species of *Rehderodendron* in the Gaoligong Shan

1a. Leaf blade base subrounded to rounded, margin glandular-serrulate; fruit 2–2.5 cm wide, 9- or 10-ribbed, pale brown . . . . 1. *R. gongshanense*
1b. Leaf blade base cuneate to subrounded, margin entire; fruit 1.7–2 cm wide, 5-ribbed, dark reddish brown . . . . 2. *R. microcarpum*

1. Rehderodendron gongshanense Y.C. Tang, Acta Bot. Yunnan. 10:350. 1988. TYPE.— CHINA. Yunnan: Gongshan Zizhixian, Dulongjiang Xiang, Qinlangdang, 1500 m [Gaoligong Shan], 11 August 1982, *Qinghai-Xizang Expedition 9227* (holotype: PE; isotype: KUN!).

Trees to 10 m tall. Young branchlets irregularly yellow-villous or glabrous; vegetative buds densely yellow-villous. Petiole 6–10 mm, yellow-villous; leaf blade elliptic to oblong, 9–20 × 4–10 cm, 2–2.3 times as long as wide, chartaceous, green both sides, sparsely yellow-villous both sides, more densely so on midvein, base subrounded to rounded, margin minutely glandular-serrulate, apex acute to short-acuminate; veins tawny to dull orange, midvein prominent abaxially, slightly sulcate adaxially, other veins slightly raised both sides, secondary veins 7–12 per side. Flowers unknown. Fruit cylindric, usually slightly crescentic, 5–7 × 2–2.5 cm, shallowly 9- or 10-ribbed, pale brown, base and apex conic-umbonate and yellow-tomentose, rest of fruit glabrous; rostrum 1–2 mm; exocarp ca. 1 mm thick. Seed 1, ca. 4 cm × 4 mm.

The only specimens of this species known to us are from the type collection.

Illustration.— Y.C. Tang, Acta. Bot. Yunnan. 10:350 t. 1. 1988.

Phenology.— Fr. Aug.

Distribution and habitat.— Subtropical evergreen broadleaf forests ("tropical rain forest" on label); ca. 1500 m. In GLGS: CHINA. Yunnan: Gongshan Xian (Dulongjiang Xiang); Figure 5. Endemic to GLGS.

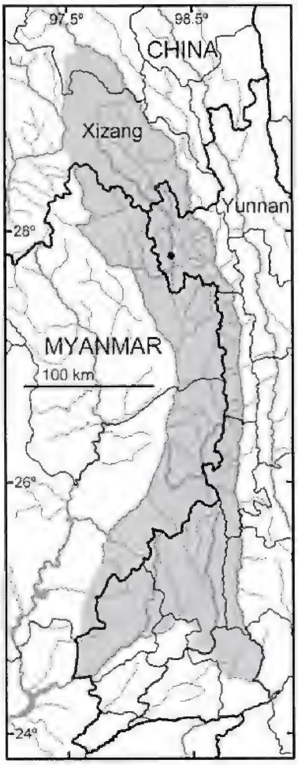


Figure 5. Distribution map of *Rehderodendron gongshanense* in the GLGS region.

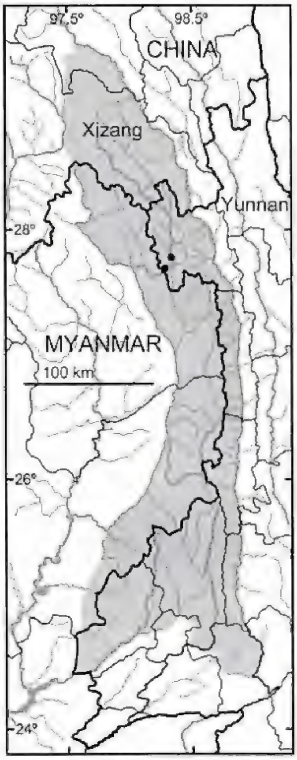
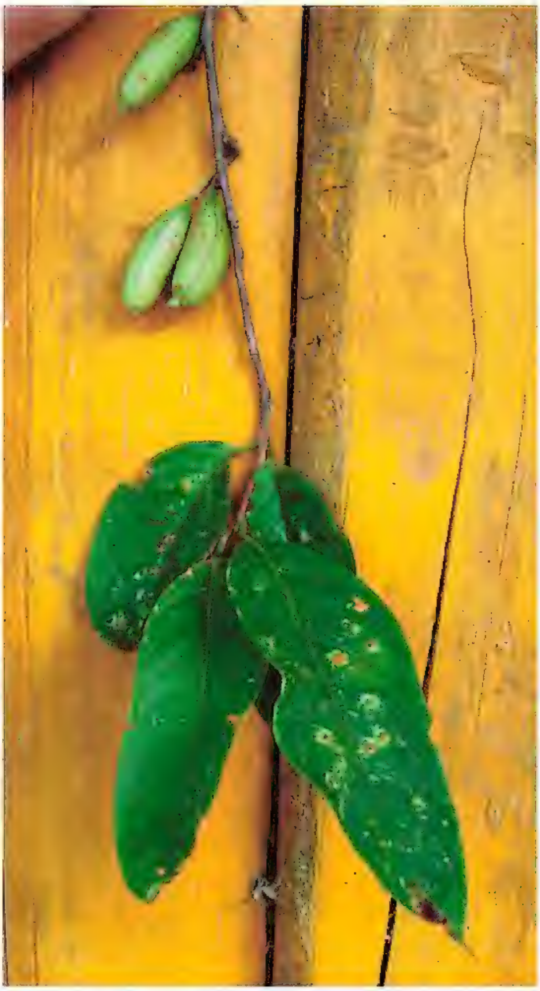


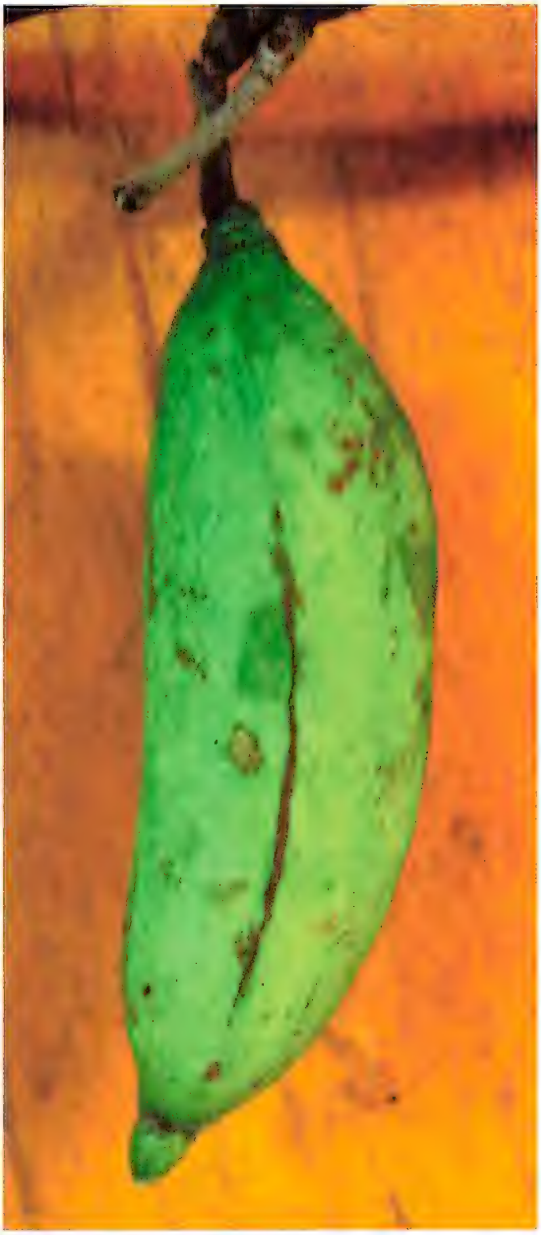
Figure 6. Distribution map of *Rehderodendron microcarpum* in the GLGS region.

Chinese name.— 贡山木瓜红 gong shan mu gua hong.

2. Rehderodendron microcarpum K.M. Feng, Fl. Yunnan. 3:410. 1983. Type.— China. Yunnan: Gongshan Zizhixian, Dulongjiang Xiang, Bank of Dulongjiang, Er Da Mu, 1400 m [Gaoligong Shan], 14 September 1956, *P.I. Mao 451* (holotype: KUN!).

Tree to 10 m tall. Young branchlets moderately grayish brown-tomentose; vegetative buds densely grayish brown-tomentose. Petiole 9–15 mm, sparsely to moderately grayish brown- or tawny yellow-tomentose; leaf blade elliptic or oblong, 14.7–17 × 5.5–6.5 cm, 2–2.8 times as long as wide, chartaceous, green both sides, sparsely to moderately yellow- or yellow-orange-villous both sides, more densely so on midvein, base broadly cuneate to subrounded, margin minutely glandular-serrulate or entire, apex short-acuminate, veins tawny to dull orange, midvein prominent abaxially, slightly sulcate adaxially, other veins slightly raised both sides, secondary veins 8–13 per side. Flowers unknown. Fruit crescentic-ellipsoid, 5.5–5.6 × 1.7–2 cm, shallowly 5-ribbed, dark reddish brown, base broadly funnelform and glabrous or moderately yellow-tomentose, apex conical and yellow-tomentose, rest of fruit glabrous or with a few scattered trichomes; rostrum 2–6 mm; exocarp ca. 1–2 mm thick; mesocarp + endocarp appearing irregularly ca. 13-ribbed in cross-section, lacunae filled with spongy parenchyma; locules 2, one deltoid and ca. 3 × 1.5 mm in cross-section, the other circular and ca. 4.5 mm diam. in cross-section. Seeds 2, one per locule.





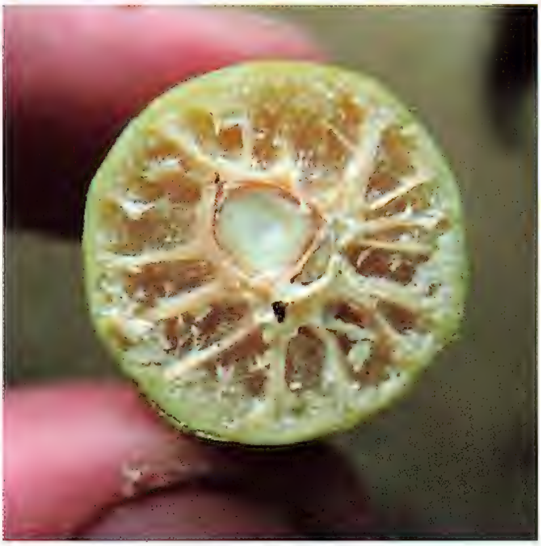


FIGURE 7 (upper left). Fruiting branchlet of *Rehderodendron microcarpum*. Photo by P.W. Fritsch.

FIGURE 8 (upper right). Fruit of *Rehderodendron microcarpum*. Photo by P.W. Fritsch.

FIGURE 9 (lower left). Cross-section of fruit of *Rehderodendron microcarpum*. Photo by P.W. Fritsch.

Illustration.— C.Y. Wu, Fl. Yunnan. 3:411 t. 117(1–3). 1983.

Photographic images.— Figures 7–9.

Phenology.— Fr. Aug–Sep.

Distribution and habitat.— Subtropical evergreen broadleaf forests ("tropical rain forest" on labels); 1270–1400 m. In GLGS: CHINA. Yunnan: Gongshan Xian (Dulongjiang Xiang); Figure 6. Endemic to GLGS.

Chinese name.— 小果木瓜红 xiao guo mu gua hong.

Additional Gaoligong Shan specimen examined: CHINA. YUNNAN: GONGSHAN ZIZHIXIAN. Dulongjiang Xiang. Ca. 0.3 direct km S of Qinglan Dang on trail to Maku, W side of the Dulong Jiang Valley, ca. 2.1 direct km WNW of Maku and ca. 2.8 direct km NE of the Myanmar border, 1270 m, 19 Aug 2006, *GLGS 32557* (CAS).

3. STYRAX Linnaeus, Sp. Pl. 444. 1753.

Type: *Styrax officinalis* L. [as *S.* "*officinale*"]

安息香属 an xi xiang shu.

Cyrta Lour., Fl. cochinch. Ed. 1:278. 1790.
Anthostyrax Pierre, Fl. forest. cochinch. sub t. 260. 1892.

Shrubs or trees, deciduous (GLGS). Fertile shoots produced both laterally and (on at least some branchlets) terminally on branchlets of previous growth period; young branchlets, petioles, and leaf blades abaxially often with stalked, short-armed orange-brown stellate trichomes (in addition to any other stellate pubescence that may be present); vegetative bud scales absent. First two leaves opposite or subopposite (GLGS); leaf blade margin entire or serrate, secondary vein axils abaxially tufted-pilose, trichomes partially covered by membranous flap of tissue (GLGS). Inflorescences racemose (GLGS). Pedicels not articulated. Calyx crowned by (4)5(6) minute teeth with valvate aestivation. Corolla lobes 5(6), with imbricate aestivation (GLGS), basally connate, spreading. Stamens 10(–12), subequal in length, adnate to ca. 2 mm or more beyond base of corolla; tube absent (GLGS); filaments pubescent (GLGS); filament trichomes with branches circular in cross-section, glossy; anther connectives not surpassing thecae (GLGS), not toothed, thecae often pubescent. Carpels 3; ovary slightly inferior, densely pubescent; ovules on average ca. 8 per carpel, irregularly arranged, bitegmic. Stylodia completely connate; stigma truncate to capitellate. Fruit capsular, loculicidally 3-valve-dehiscent (GLGS), globose to ellipsoid or ovoid (GLGS), 7–18 mm (GLGS); exocarp not ribbed; mesocarp present; fruiting calyx epicarpous only slightly beyond fruit base. Seed 1(–3), globose or ellipsoid, 7–16 mm (GLGS), with a broad hilum; seed coat indurate, reticulate.

A genus of ca. 130 species distributed in the Americas (from the U.S.A. to Argentina), the eastern Mediterranean region, and eastern and southeastern Asia; 2 species in China, 0 endemic [Hwang and Grimes (1996); Huang et al. (2003)]; 6 species in Myanmar, 1 endemic [Kress et al. (2003); Huang et al. (2003); P.W. Fritsch, unpubl. data]; 2 species in GLGS, 0 endemic.

Within *Styrax*, Li et al. (2000) recognized *S. grandiflorus*, *S. perkinsiae*, and *S. roseus* from the GLGS, all of which are included in *S.* ser. *Cyrta* of section *Imbricatae* (*sensu* Fritsch 1999). In a detailed taxonomic revision of the "imbricate group" within this series (i.e., species of ser. *Cyrta* with imbricate floral aestivation), Huang et al. (2003) placed *S. grandiflorus* under synonymy of *S. japonicus*. They also placed *S. perkinsiae* and *S. roseus* [as well as *S. macranthus* and possibly *S. bashanensis*, recognized along with these in Hwang and Grimes (1996)] as synonyms under *S. hookeri*, the latter considered prior to their treatment as restricted to areas west of the GLGS. We follow the treatment of Huang et al. (2003) and recognize two species of *Styrax* from the GLGS.

Key to Species of *Styrax* in the Gaoligong Shan

1a. Leaf blades abaxially densely tomentose or rarely subglabrous; pedicels 4–12 mm long; calyx 7–10 mm; at least basal third of style pubescent; fruit apex obtuse to rounded; seeds with 3 furrows, smooth . . . . 1. *S. hookeri*

1b. Leaf blades abaxially sparsely tomentose; longer pedicels 13–32 mm long; calyx 4–6 mm; style glabrous except at very base; fruit apex conical; seeds with 3 furrows alternating with 3 ridges, finely verrucose at least on ridges . . . . 2. *S. japonicus*

1. Styrax hookeri C.B. Clarke in Hook. f., Fl. Brit. India 3:589. 1882 (as *S.* "*Hookeri*"). TYPE.— INDIA. Sikkim: 6000–7000 ft., *J. D. Hooker s.n.* (lectotype, designated by Huang et al. 2003: K!; isotypes: BM!, BR!, C!, K!, L[2]!).

Styrax macranthus Perkins, Bot. Jahrb. Syst. 31:487. 1902. TYPE.— CHINA. Yunnan: Lüchun Xian, region of Feng Chun Ling, 7000 ft. [2000 m, protologue], S of the Red River, *A. Henry 10644* (lectotype, designated by Huang et al. 2003: K!; isotypes: A!, BM!, E[2]!, IBSC[2]!, MO!, PE!).

Styrax caudatus Perkins in Engl., Pflanzenr. IV. 241 (Heft 30):74. 1907. TYPE.— INDIA. Assam: Mt. Sillet (Perkins 1907), *Wallich 4400B* (holotype: B destroyed; isotype: K).

Styrax hookeri C.B. Clarke var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8:84. 1910. TYPE.— CHINA. Yunnan: Zhaotong Shi, Hay Tse Pa, 6 July 1906, *F. Ducloux 4626* (lectotype, designated by Huang et al. 2003: P!).

Styrax roseus Dunn, Bull. Misc. Inform. Kew 1911:273. 1911. TYPE.— CHINA. Sichuan: Ebian Yizu Zizhixian, Mt. Wu [from protologue], Wa-shan (Rehder 1912), 8000 ft. [2600 m, protologue], July 1903, *E.H. Wilson 4065* (holotype: K!; isotypes: A[2]!, BM!, IBSC!).

Styrax perkinsiae Rehder in Sargent, Pl. Wilson. 1:292. 1912 [as *S.* "*Perkinsiae*"]. TYPE.— CHINA. Sichuan: Ebian Yizu Zizhixian, Wa-shan, 6000–7000 ft. [2000 m, protologue], 1908, *E.H. Wilson 2576* (lectotype, designated by Huang et al. 2003: A!; isotypes: BM!, E!).

Styrax shweliensis W.W. Smith, Notes Roy. Bot. Gard. Edinburgh 12:236. 1920. TYPE.— CHINA. Yunnan: Tengchong Xian, [Sanyun Xiang], Tengyueh-Shweli divide; 25° N, 7000 ft. [Gaoligong Shan], May 1913, *G. Forrest 9869* (holotype: E!; isotypes: A!, K!).

Shrubs or trees to 10 m tall. Young branchlets sparsely to densely white-, tawny, or golden-orange-tomentose; vegetative buds grayish brown, orange-, golden brown-, or orange-brown-tomentose. Petiole 2–13 mm, at least sparsely tomentose or villous; leaf blade oblong, ovate, oblong-obovate, lanceolate-ovate, or elliptic, 5–16.5 × 2.3–9.3 cm, 1.4–2.6 times as long as wide, chartaceous, abaxially pale green to glaucous, densely white-tomentose or rarely subglabrous, less pubescent on veins, adaxially green to dark green, sparsely tomentose to appressed-pilose, more densely so on midvein and secondary veins, base often slightly oblique, subrounded to broadly cuneate, rarely shallowly cordate or narrowly cuneate, margin glandular-serrulate, apex acuminate to caudate, midvein prominent abaxially, plane or slightly sulcate adaxially, secondary veins 5 to 7 per side, smaller veins raised both sides, tertiary veins usually notably conspicuous. Fertile shoots 5–13 cm, 3- to 5-leaved. Lateral inflorescences 1- to 3-flowered; pseudoterminal inflorescences 1- or 2-flowered or racemose, 4–9 cm, (1-)2- or 3- (to 6-)flowered, rachis yellowish brown-, grayish brown-, or orangish-brown-tomentose or -pilose; pedicels 4–12 mm long, tomentose or villous. Flowers 1.8–2.6 cm. Calyx 7–10 × 5–9 mm, grayish green- or yellow-tomentose, also with various amounts of larger scattered grayish green, tawny, orange, or brown stiff trichomes especially proximally, within 2 mm from margin more sparsely pubescent, somewhat scarious, brown when dry; calyx teeth deltoid to linear-deltoid, to 1 mm, not contiguous, margin truncate, undulate, or irregularly 2- or 3-lobed between the teeth. Corolla 1.7–2 cm, white, tube 3–4 mm, lobes (4)5, obovate to obovate-elliptic, 11–16 × 5–9 mm, densely appressed-pubescent on both sides or sometimes sparsely so adaxially, apex obtuse. Stamen filaments 5–7 mm, straight, proximally white-villous especially along margin, distally attenuate and glabrous or nearly so; anthers 4–6.5 mm, thecae equal to or slightly exceeding connective. Style 15–22 mm, at least basal third white-pubescent. Fruiting calyx 4–10 × 10–16 mm. Fruit subglobose or ovoid, 7–15 × 7–13 mm, dehiscent from base or apex, apex obtuse to rounded, apiculate rostrum distinct; pericarp 0.1–0.3(–0.6) mm thick, dry, ± rugose and often faintly longitudinally striate, light gray, grayish green-, grayish brown-, yellow-, or orange-tomentose. Seeds subglobose or ovoid, 7–15 × 7–13 mm, beige or brown, 3-furrowed, smooth, glabrous.

Selected illustrations.— S.M. Hwang, Fl. Reipubl. Popularis Sin. 60(2):90 t. 30(6–9). 1987 (as *S. perkinsiae*); ibid.:101 t. 34(6–10). 1987 (as *S. macranthus*); ibid.:103 t. 35(1–6). 1987 (as *S. roseus*); C.Y. Wu & P.H. Raven, Fl. China. Ill. 15:199, t. 199(6–9). 2000 (as *S. perkinsiae*); ibid.:203 t. 203(7–12). 2000 (as *S. macranthus*); ibid.:204 t. 204(1–7). 2000 (as *S. roseus*); Figure 10.

Photographic image.— Figure 11.

Phenology.— Fl. May–Jul, fr. Aug–Oct.

Distribution and habitat.— Coniferous forests, subtropical evergreen broadleaf forests, mixed evergreen and deciduous broadleaf forests, deciduous broadleaf forests ("tropical rain forest" on some labels), along rivers and streams, along ridges, valleys, thickets, meadows; 1500–3450 m. In GLGS: CHINA. Xizang: Zayü Xian (Tsarong Xiang). Yunnan: Fugong Xian (Jiakedi Xiang, Lishadi Xiang), Gongshan Zizhixian (Bingzhongluo Xiang, Cikai Zheng, Dulongjiang Xiang), Lushui Xian (Pianma Xiang), Tengchong Xian (Houqiao Zheng, Mingguang Xiang, Sanyun Xiang), MYANMAR (state uncertain); Figure 12. Outside of GLGS: Guangxi, Guizhou, Sichuan, Xizang, Yunnan [Bhutan, India, Myanmar, Nepal].

Chinese name.— 禄春安息香 lu chun an xi xiang.

Additional Gaoligong Shan specimens examined: CHINA. XIZANG: ZAYÜ XIAN. Tsarong Xiang. Salwin-Kiu-chiang divide, Jul 1919, *F 18957* (A, E, K); Salwin-Kiu Chiang divide, 10000–11000 ft., Sep 1921, *F 20300* (E, K); same locality, Oct 1921, *F 20855* (E, K); Salwin-Kui Chiang divide, W of Chamutong, 9000 ft., Jun 1922, *F 21803* (E, P); same locality, Oct 1922, *F 22927* (E, K); Salwin-Kiu-chiang divide, Jun 1924, *F 25649* (BM); Mount Kenyichunpo and region of Champutong, Salween-Irrawadi watershed, 9500 ft., 1923, *J.F.C. Rock 10243* (A); Mt. Kenichunpo, E and W slopes, Salwin and Irrawady divide, mtns. of Champutong, 11000 ft., May–Jul 1932, *J.F.C. Rock 22044* (A, BM, E); Salween-Kiukiang Divide, Qi Ming Shui, 3000 m, 12 Jul 1938, *T.T. Yü 22079* (E, KUN) [label states "Yunnan" but may be in Xizang]; Salwin-Kiukiang Divide, E of Tehatu, 2850 m, 15 Sep 1938, *T.T. Yü 20294* (A, E, KUN) [label states "Yunnan" but may be in Xizang]. **YUNNAN:** Gaoligongshan E slope, 2840 m, 24 May 1960, *Nanshui Team 9051* (KUN). **FUGONG XIAN. Jiakedi Xiang.** Gu Quan Da Dui Qiao Mi Gu Lu, 2600 m, 10 Jun 1982, *Qinghai-Xizang Expedition 7245* (KUN); Che-tse-lo, 3200 m, 4 Sep 1934, *H.T. Tsai 58355* (A); same locality, 9 Sep 1934, *H.T. Tsai 58439* (A, KUN). **Lishadi Xiang.** Between the Shibali Logging Station and Yaping Pass, ca. 2 km W of Shibali, rd from the Nujiang to Yaping Pass, E side of Gaoligong Shan, 2757 m, 9 May 2004, *GLGS 20485* (CAS); between the Shibali Logging Station and Yaping Pass, ca. 4.5 km W of Shibali, rd from the Nujiang to Yaping Pass, E side of Gaoligong Shan, 2700 m, 9 May 2004, *GLGS 20498* (CAS); Yaduo Cun, above Shibali, S side of N fork of Yamu He, rd to the Myanmar border at Yaping Yakou, E side of Gaoligong Shan, 2830 m, 6 Aug 2005, *GLGS 26539* (CAS); Yaduo Cun, vicinity of Shibali, N side of N fork of Yamu He, E side of Gaoligong Shan, 2470 m, 9 Aug 2005, *GLGS 26764* (CAS); Yaduo Cun, above Shibali to the Myanmar border at Yaping Yakou, N side of N fork of Yamu He, E side of Gaoligong Shan, 2750 m, 10 Aug 2005, *GLGS 26892* (CAS); same data, *GLGS 26916* (CAS); Yaduo Cun, above Shibali, N side of S fork of Yamu He, E side of Gaoligong Shan, 2900 m, 15 Aug 2005, *GLGS 27284* (CAS); Yaduo Cun, above Shibali, N side of S fork of Yamu He, E side of Gaoligong Shan, 2800 m, 15 Aug 2005, *GLGS 28339* (CAS). **GONGSHAN ZIZHIXIAN. Bingzhongluo Xiang.** Upper middle region of Bingzhongluo River, 2500–3450 m, 3 Aug 1979, *X.F. Deng 791361* (KUN [2]); Chang Pu Tong, 2000–2300 m, 5 Sep 1940, *K.M. Feng 7455*

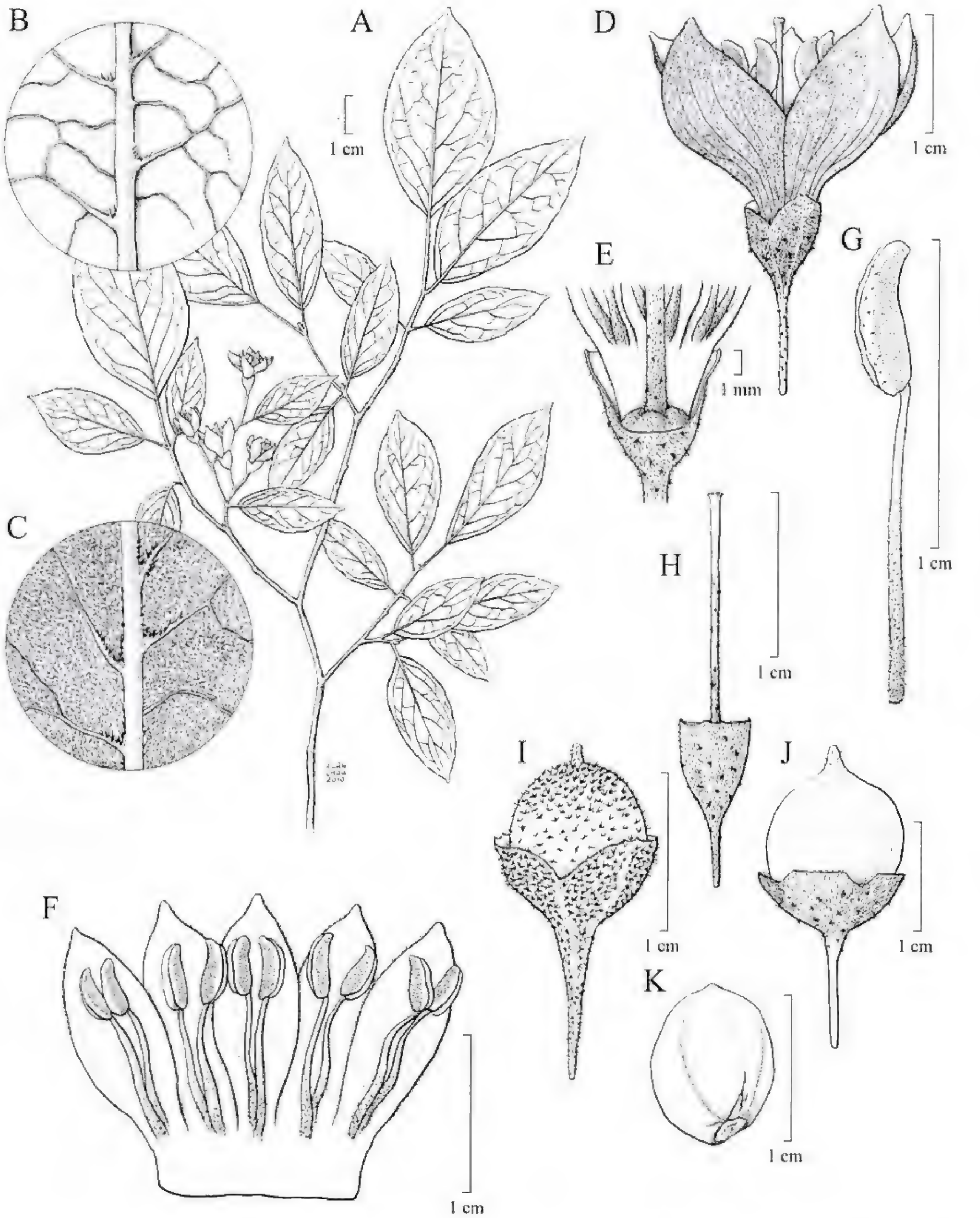


FIGURE 10. *Styrax hookeri*. - A. Flowering branch. - B. Close-up of abaxial leaf surface. Note glabrous condition on this specimen except in axils of secondary veins *(cf.* subfigure C). - C. Close-up of densely tomentose abaxial leaf surface, the common condition in the Gaoligong Shan (*cf.* subfigure B). - D. Flower. Note deeply lobed calyx (*cf.* subfigure H). - E. Flower with ventral portion cut away showing ovary, style base, and inner-proximal portion of corolla and androecium. - F. Corolla and androecium. - G. Stamen. - H. Calyx, style, and stigma. Note merely toothed calyx *(cf.* subfigure D). - I. Persistent calyx and fruit. - J. Persistent calyx and fruit (*cf.* subfigure I). - K. Seed. A, C–D, G based on *GLGS (H. Li) 11989* (CAS); B, J based on *GLGS 31805* (CAS); E based on *G. Forrest 30908* (E); F, H based on *GLGS 30519* (CAS); I based on *GLGS 27284* (CAS); K based on *GLGS 31740* (CAS). (Drwaings by Alan Chou.)

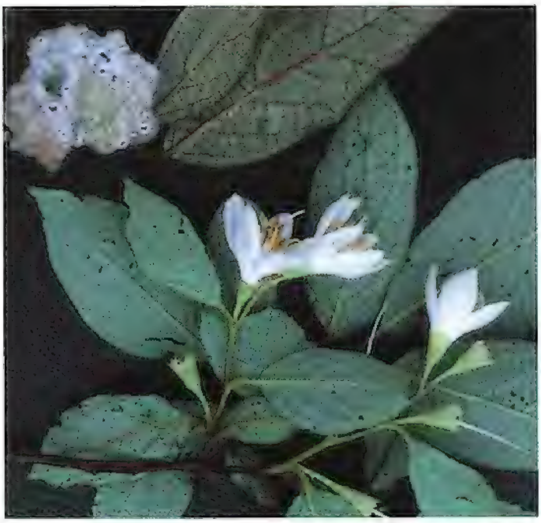


FIGURE 11. Flowering and galled branches of *Styrax hookeri*. (Photo by P.W. Fritsch.)

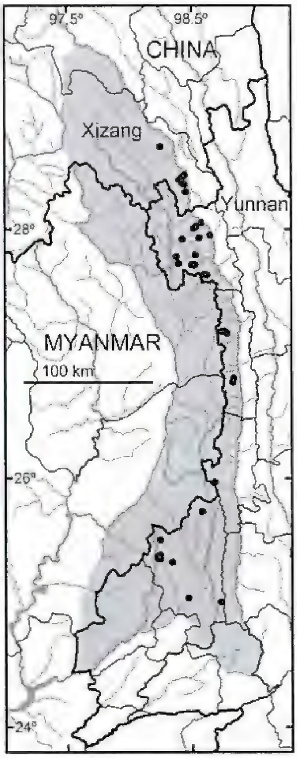


FIGURE 12. Distribution map of *Styrax hookeri* in the GLGS region.

(KUN); Si Ji Tong, 2700–3000 m, 20 Sep 1940, *K.M. Feng 7938* (KUN); vicinity of Fucai, N side of Nianwaluo He, ca. 11.3 direct km WSW of Bingzhongluo, E side of Gaoligong Shan, 2830 m, 1 Sep 2006, *GLGS 31740* (CAS); vicinity of Yidongwei below the Fucai camp, N side of Nianwaluo He, ca. 9.2 direct km W of Bingzhongluo, E side of Gaoligong Shan, 2530 m, 1 Sep 2006, *GLGS 31805* (CAS). **Cikai Zheng.** Hei Pu Shan, 7 Oct 1940, *K.M. Feng 8236* (KUN); track from Qi Qi Nature Reserve Station towards Dong Shao Fang, 2600 m, 21 Sep 1997, *GLGS 9518* (E, KUN); E side of Gaoligong Shan, along the Danzhu He, rd from Nu Jiang at Danzhu to Myanmar border, 2650 m, 2 Jul 2000, *GLGS 11906* (CAS, KUN); same data, *GLGS 11907* (CAS [2], KUN); E side of Gaoligong Shan, along the Danzhu He, rd from Nu Jiang at Danzhu to Myanmar border, 2900 m, 5 Jul 2000, *GLGS 11989* (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, Jidu, vicinity of Qiqi above the Pula He, 2570 m, 12 Jul 2000, *GLGS 12477* (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, trail from Qiqi to Dongshao Fang and the pass to the Dulong Jiang Valley, 2830 m, 17 Jul 2000, *GLGS 12784* (CAS, KUN); E side of Gaoligong Shan, W of Gongshan, trail from Qiqi to Dongshao Fang and the pass to the Dulong Jiang Valley, 2700 m, 17 Jul 2000, *GLGS 12792* (CAS, KUN). **Dulongjiang Xiang.** Prope fines Tibeto-Birmanicus in convalle fluvii Djiou-djiang (Irrawadi or. sup.), supra vicum Schutsche, 2800–2900 m, 9 Jul 1916, *H. F. v. Handel-Mazzetti 9456* (K); from Gongshan to Dulongjiang, Da Ba Di, 2500 m, 6 Sep 1956, *P.I. Mao 427* (KUN); A Lu La Ka Long Po, 2600 m, 6 Jun 1960, *Nanshui Team 9239* (KUN); Long Yuang, 2400 m, 26 Aug 1982, *Qinghai-Xizang Expedition 9653* (KUN). **LUSHUI XIAN. Pianma Xiang.** Hpimaw, 8800 ft., 1 Oct 1919, *R.J. Farrer 1344* (E); new rd from Pianma Pass to Pianma, 3200 m, 18 Aug 1964, *S.K. Wu 8478* (KUN). **TENGCHONG XIAN.** Lava bed W of Tengyueh, 5000 ft., May 1912, *F 7685* (E, K); *F 21112* (P); 1931, *F 30908* (BM, E). **Houqiao Zheng.** Xiajie Cun, vicinity of Baliwenguan, ca. 7.3 direct km NW of Houqiao (Guyong), 1910 m, 28 May 2006, *GLGS 30755* (CAS); Hou Qiao Gong Sha, mtns. in Hei Ni Tang, 1850 m, 19 May 1964, *Wu 6670* (KUN); Guyong Dai Zha, Jian Gou Shan, Wa river mouth, 7400 m, 1 Jun 1964, *S.K. Wu 6988* (KUN); rd from Qi Pan Shi to Zi Mei Shan, 3000 m, 17 Jun 1964, *S.K. Wu 7203* (KUN); Lang Ya Shang, 1 Apr 1980, *D.Y. Xia BG–58* (KUN). **Mingguang Xiang.** Zizhi Cun. Ca. 1 km NW of Zizhi in Jiangao Shan, rd from Zizhi to Baduolin Yakou (pass at marker number 8 between China and Myanmar) W of Gaoligong Shan, 1980 m, 23 May 2006, *GLGS 30519* (CAS). **Sanyun Xiang.** Tengyueh-Shweli divide, 7000 ft., May 1913, *F 18504* (A, E, K). **MYANMAR.** E Upper Burma, 7000 ft., Jun 1924, *F 24681* (K).

2. **Styrax japonicus** Siebold & Zuccarini, Fl. Jap. 1:53. 1837–1838 (as *S.* "*japonicum*"). *Cyrta japonica* (Siebold & Zuccarini) Miers, Ann. Mag. Nat. Hist., ser. 3, 3:279. 1859. Type.— Japan. Kyushu: Kumamoto Pref., Simabara, *I. Keiske s.n.* (lectotype, designated by Huang et al. 2003: L; digital image of lectotype!).

Styrax grandiflorus Griffith, Not. Pl. Asiat. 4:287. 1854 [as *S.* "*grandiflora*"]. Type.— Myanmar [Sagaing Division] or India [Assam]: Naga Hills, Namtuzeeh [March 1837, protologue] and Nempea [19 March 1837, protologue], *W. Griffith 3671* (Perkins 1907) (holotype: K!; isotype: GH!).

Styrax cavaleriei H. Léveillé, Repert. Spec. Nov. Regni Veg. 4:331. 1907 [as *S.* "*Cavaleriei*"]. Type.— China. Guizhou: Longli Xian, 7 May 1903, *J. Cavalerie 997* (holotype: E!; isotype: A!).

Styrax bodinieri H. Léveillé, Repert. Spec. Nov. Regni Veg. 4:332. 1907 [as *S.* "*Bodinieri*"]. Type.— China. Guizhou: Guiyang Shi, vicinity of Guiyang, Collège Mt., April 1898, *E. Bodinier 2221* (holotype: E!; photo of holotype: A!).

Styrax duclouxii Perkins, Repert. Spec. Nov. Regni Veg. 8:83. 1910 [as *S.* "*Duclouxii*"]. Type.— China. Yunnan: Nanjian Yizu Zizhixian, near Lanngy Tsin, 20 April 1904, *F. Ducloux 2716* (lectotype, designated by Huang et al. 2003: P!).

Styrax touchanensis H. Léveillé, Repert. Spec. Nov. Regni Veg. 11:64. 1912. Type.— China. Guizhou: Dushan Xian, April 1902, *E. Bodinier s.n.* (holotype: E!; isotypes: A!, E!).

Shrubs or trees to 10(–15) m tall. Young branchlets sparsely grayish yellow- or pale yellow-tomentose or -villous; vegetative buds brown-tomentose or -villous. Petiole 2–10 mm, at least sparsely tomentose or villous; leaf blade elliptic, oblong-elliptic, oblanceolate-elliptic, or subrhombic, 5.5–12 × 3.1–7 cm, 1.6–2.8 times as long as wide, chartaceous to thick-chartaceous, abaxially light green, very sparsely tomentose, more densely so on midvein, adaxially dark green, sparsely tomentose especially on veins or glabrous, base cuneate to broadly cuneate or subrounded, often decurrent into petiole, margin distally glandular-serrulate, otherwise entire, apex acute to short-acuminate, midvein prominent abaxially, plane or slightly sulcate adaxially, secondary veins 4 to 7 per side, smaller veins raised abaxially and usually adaxially, tertiary veins not notably conspicuous. Fertile shoots 7–12 cm, 1- to 4-leaved. Lateral inflorescences 1- or 2-flowered; pseudoterminal inflorescences 2-flowered or racemose, 4–9 cm, 2- to 5-flowered, rachis yellow- or orange-villous; longer pedicels 13–32 mm, tomentose. Flowers 1.5–2.7 cm. Calyx 4–6 × 4–6 mm, densely white- or grayish yellow-pilose or -tomentose, within 1–2 mm from margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; calyx teeth deltoid, 0.3–0.8 mm, not contiguous, margin ± straight or somewhat irregular between the teeth. Corolla 1.2–2 cm, white or occasionally tinged with pink, tube 3–5 mm, lobes 5(6), oblong-elliptic, oblong-ovate, or oblong-lanceolate, 11–15 × 5–9 mm, densely appressed-pubescent on both sides or sometimes sparsely so adaxially, apex obtuse. Stamen filaments 5–6 mm, straight, proximally white-villous, distally attenuate and glabrous; anthers 4–7 mm, connective usually slightly exceeding thecae, occasionally subequal. Style 13–18 mm, glabrous except at very base. Fruiting calyx 5–9 × 10–12 mm. Fruit ovoid or ellipsoid, 10–18 × 9–10 mm, dehiscent usually from base, apex conical, apiculate rostrum tapering into fruit body; pericarp 0.4–1.0 mm thick, dry, coarsely and irregularly rugose, gray- or grayish yellow-tomentose. Seeds ellipsoid, 10–16 × 6–8 mm, brown, longitudinally 3-furrowed, the furrows alternating with 3 ridges, finely verrucose at least on ridges, glabrous. n > 20 (Manshard 1936), 8 (Yamazaki 1993).

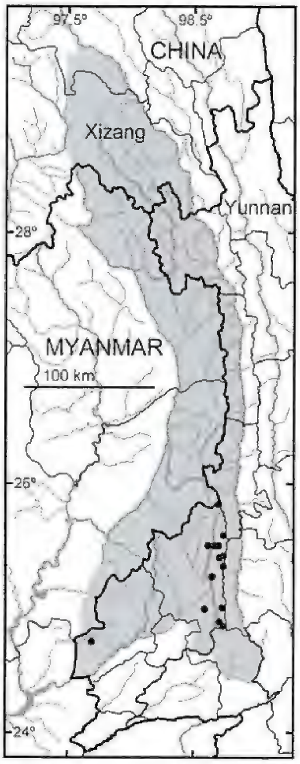


Figure 13. Distribution map of *Styrax japonicus* in the GLGS region.

Selected illustrations.— Griff., Ic. Pl. Asiat. 4: t. 423. 1854 (as *S. grandiflorus*); C.Y. Wu, Fl. Yunnan. 3:428 t. 122(1–10). 1983

(7–10 as *S. grandiflorus*); S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2):93 t. 31(1–11). 1987 (8–11 as *S. grandiflorus*); C. Y. Wu & P. H. Raven, Fl. China. Ill. 15:200 t. 200(1–11). 2000 (8–11 as *S. grandiflorus*).

PHENOLOGY.— Fl. Apr–Jul, Fr. Aug–Nov.

DISTRIBUTION AND HABITAT.— Subtropical evergreen broadleaf forests, woodlands, canyons, ravines, riparian situations, thickets; 1500–2700 m. In GLGS: CHINA. Yunnan: Longling Xian, Tengchong Xian (Dongshan Xiang, Jietou Xiang, Qushi Xiang, Sanyun Xiang, Wuhe Xiang), Yingjiang Xian (Xima Xiang); Figure 13. Outside of GLGS: Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shandong, Shanxi, Sichuan, Taiwan, Yunnan, and Zhejiang [Japan, Laos, Myanmar, North Korea, Philippines, South Korea, Vietnam].

CHINESE NAME.— 野茉莉 ye mo li.

ADDITIONAL GAOLIGONG SHAN SPECIMENS EXAMINED: CHINA. YUNNAN: LONGLING XIAN. 1750 m, 15 Apr 1934, *H.T. Tsai 55793* (A, BO, KUN); Tian Ying Si, 2500 m, 10 Aug 1941, *C.W. Wang 90046* (KUN). **TENGCHONG XIAN.** Oct 1917, *F 16049* (E); Jun 1918, *F 17521* (A, E). **Dongshan Xiang.** Qingcaitang, old rd from Tengchong to Baoshan between Tengchong and the Longchuan Jiang, 2010 m, 2 Nov 1998, *GLGS 11357* (CAS, KUN). **Jietou Xiang.** Shweli Valley, 6000 ft., May 1913, *F 11945* (A, BM, MO); Shweli-Salwin divide, 9000 ft., Jul 1917, *F 15710* (A, E); Shweli-Salwin divide, 8000–9000 ft., Apr 1924, *F 24039* (E); same locality, Jun 1924, *F 24445* (AAU, BM, E, K, MO); Shweli-Salwin divide, 9000–10000 ft., Sep 1924, *F 25191* (E); Shweli-Salwin divide, N of Ho-lou, 9000 ft., May 1925, *F 26380* (A, E, K); Shaba Cun, vicinity of Yangjia Shan Jiao, W side of Gaoligong Shan, 1900 m, 15 May 2006, *GLGS 28175* (CAS). **Qushi Xiang.** Shweli-Salwin divide, 8000–9000 ft., Nov 1925, *F 27397* (E). **Sanyun Xiang.** Shweli-Salwin divide, 7000 ft., Jun 1919, *F 17899* (A, E); Shweli-Salwin divide, 7000 ft., Sep 1919, *F 18455* (A, E); hills E of Tengyueh, 7000–8000 ft., Apr 1931, *F 29552* (E); same locality, Jul 1931, *F 29792* (AAU, E). **Wuhe Xiang.** Zhonglin, Jintang Village, W side of Gaoligong Shan, 1530 m, 24 May 2005, *GLGS 24810* (CAS); valley on W side of Zhengding Forest Reserve Station, W side of Gaoligong Shan, 1869 m, 27 May 2005, *GLGS 24978* (CAS). **YINGJIANG XIAN. Xima Xiang.** Gong She Ba Yan Po, 1600 m, 2 Nov 1974, *G.D. Tao 13063* (KUN).

ACKNOWLEDGMENTS

We thank the curators of the herbaria listed in the materials and methods section, who kindly made specimens available, Jon Fong (CAS) for technical help with the collection database, Lihua and Alice Zhou for data entry, label interpretation, and translation to Ghinese, and Martyn Dickson (RBGE) for the photographic image of *Huodendron biaristatum*, Bruce Bartholomew (CAS) for preparing the distribution maps and assistance in georeferencing, and Alan Chou for the illustration (Fig. 10). This work was supported by U.S. National Science Foundation grant DEB-0103795 to the first author and grant 08-90235-000-GSS from the MacArthur Foundation.

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Appendix 1

List of Species

1-1. *Huodendron biaristatum* (W.W. Smith) Rehder
1-2. *Huodendron tibeticum* (J. Anthony) Rehder
1-3. *Huodendron tomentosum* Y.C. Tang ex S.M. Hwang
2-1. *Rehderodendron gongshanense* Y.C. Tang
2-2. *Rehderodendron microcarpum* K.M. Feng
3-1. *Styrax hookeri* C.B. Clarke
3-2. *Styrax japonicus* Siebold & Zuccarini

Appendix 2

Index to Exsiccatae

All specimens examined by the authors are listed alphabetically by collector, followed by collection numbers (and herbarium if anonymous). Numbers in parentheses correspond to those in the numerical list of species.

Bijiang Expedition 738 (1-2).
X.F. Deng 791361 (3-1).
R.J. Farrer 1344 (3-1).
F 7685 (3-1); 9869 (3-1); 11945 (3-2); 15710 (3-2); 16049 (3-2); 17521 (3-2); 17894 (1-1); 17899 (3-2); 18020 (1-1); 18400 (1-1); 18455 (3-2); 18504 (3-1); 18833 (1-1); 18957 (3-1); 20300 (3-1); 20855 (3-1); 21112 (3-1); 21803 (3-1); 22882 (1-2); 22927 (3-1); 24039 (3-2); 24381 (1-1); 24445 (3-2); 24681 (3-1); 25191 (3-2); 25649 (3-1); 26108 (1-1); 26380 (3-2); 27397 (3-2); 29552 (3-2); 29792 (3-2); 30908 (3-1).
K.M. Feng 7455 (3-1); 7938 (3-1); 8024 (1-2); 8236 (3-1); 24729 (1-2).
GLGS 9518 (3-1); 11357 (3-2); 11906 (3-1); 11907 (3-1); 11989 (3-1); 12472 (1-2); 12477 (3-1); 12784 (3-1); 12792 (3-1); 14945 (1-2); 15221 (1-2); 17274 (1-1); 19467 (1-2); 20485 (3-1); 20498 (3-1); 21998 (1-1); 22102 (1-1); 24631 (1-1); 24810 (3-2); 24819 (1-1); 24978 (3-2); 25059 (1-1); 25207 (1-1); 26539 (3-1); 26764 (3-1); 26892 (3-1); 26916 (3-1); 27284 (3-1); 27335 (1-2); 27469 (1-2); 27688 (1-1); 27924 (1-2); 28175 (3-2); 28339 (3-1); 30239 (1-1); 30404 (1-1); 30519 (3-1); 30755 (3-1); 31740 (3-1); 31805 (3-1); 32557 (2-2).
H.F. v. Handel-Mazzetti 9456 (3-1).
P.Y. Mao 427 (3-1); 451 (2-2); 554 (1-2).
Nanshui Team 9051 (3-1); 9239 (3-1).
Qinghai-Xizang Expedition 7106 (1-2); 7245 (3-1); 7949 (1-3); 8125 (1-2); 9227 (2-1); 9249 (1-2); 9653 (3-1).
J.F.C. Rock 10243 (3-1); 22020 (1-2); 22044 (3-1); 22474 (1-2).
G.D. Tao 13063 (3-2).
H.T. Tsai 55793 (3-2); 58355 (3-1); 58439 (3-1); 59060 (1-2); 59095 (1-2).
Q.W. Wang 90046 (3-2).
S.K. Wu 6670 (3-1); 6988 (3-1); 7203 (3-1); 8293 (1-2); 8478 (3-1).
D.Y. Xia BG–58 (3-1).
T.T. Yü 19154 (1-2); 20294 (3-1); 22079 (3-1).

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Sciaphila ledermannii (Triuridaceae), a Biogeographically Significant Holosaprophyte Newly Reported from Príncipe in the Gulf of Guinea

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The holosaprophyte *Sciaphila ledermannii* (Triuridaceae) is newly reported from the oceanic island Príncipe off the western coast of tropical Africa. This is the first report of Triuridaceae among the islands in the Gulf of Guinea. *Sciaphila ledermannii* is the first holosaprophyte known from the Republic of São Tomé and Príncipe and the second known among the islands in the Gulf of Guinea. Its presence on Príncipe provides additional evidence for islands in the Gulf of Guinea likely forming part of an African pre-Pleistocene refugium.

At least 36 species of holosaprophytes, in four unrelated families, have been reported from continental Africa (Cheek and Williams 1999; Cheek 2003a, 2003b). Triuridaceae are an entirely holosaprophtytic family, represented in Africa by six species in four genera. One of them, *Sciaphila ledermannii* Engl., is herewith newly reported from the oceanic island of Príncipe in the Gulf of Guinea. This represents the first report of a holosaprophyte in the nation of São Tomé and Príncipe and the first report of any Triuridaceae among the islands in the Gulf of Guinea.

The four major islands in the Gulf of Guinea (Annobón, Bioko, Príncipe, and São Tomé) are all volcanic in origin and lie along the Cameroon line, a linear zone of weakness in the Earth's crust along which Mt. Cameroon and the Cameroon Highlands also occur on the African continent. The islands vary in age, size, distance from the continent, elevation, past connections to the mainland (i.e., continental vs. oceanic islands), and species compositions (Daniel and Figueiredo 2009). Of the three major oceanic islands in the Gulf of Guinea, Príncipe is the oldest (ca. 31 mybp) and closest to continental Africa (210 km). It is 128 sq. km in size and attains an elevation of 948 m.

Holosaprophytes are technically achlorophyllous mycotrophs (or mycoheterotrophs) because they are dependent on symbiotic fungi to provide metabolites from dead/decaying matter. Cheek and Williams (1999) showed that in Africa a disproportionate number of holosaprophytic species occur in the Gulf of Guinea region. For example, 16 species have been recorded from Cameroon (with 12 occurring on Mt. Cameroon) and 11 are known from Nigeria. The only holosaprophyte previously known from the islands in the Gulf of Guinea is the widespread (three continents and numerous islands) terrestrial orchid, *Epipogium roseum* (D. Don) Lindl., on Annobón (Exell 1973; Cheek and Williams 1999). Cheek and Ndam (1996) and Cheek and Williams (1999) proposed that a regional concentration of saprophytes is likely indicative of a refugial area, and that such concentrations are present in forests of the Gulf of Guinea region (at least on mainland Africa). Indeed, the younger (ca. 13 mybp) oceanic island São Tomé has been postulated to have been an important climatic refuge for *Begonia* since the Miocene (Plana et al. 2004). It remains unknown whether recently discovered occurrences of *Sciaphila ledermannii* on Príncipe represent remnants of a formerly wider distribution of the species or the result of one or more relatively recent dispersal events. In either case, the species had to disperse from or to Príncipe. Because Triuridaceae lack obvious mechanisms for either wind or animal dispersal of their seeds (Cheek and Williams 1999), rafting would appear to be a likely method of dispersal from the African continent to the oceanic islands in the Gulf of Guinea. The orientation of major rivers, oceanic currents, and island locations make rafting from either Nigeria/Cameroon or Angola/Congo/Gabon possible. Such a scenario has been proposed for both plants (e.g., *Elytraria*; Wenk and Daniel 2009) and animals (amphibians; Measey et al. 2007).

Cheek and Williams (1999) noted that most species of African holosaprophytes: 1) consist of rare perennial herbs, 2) have restricted distributions, 3) are confined to lowland and montane evergreen forests, and 4) often occur in shaded leaf litter along streams where the annual rainfall is in excess of 2000 mm. Two populations of *Sciaphila ledermannii* were encountered in 2010 along two separate river-systems on Príncipe. A population along the Rio Papagaio consisted of fewer than 20 individuals within 1 m^2, and a population along the Ribeira São Tomé consisted of about 50 individuals within 40 m^2. Although *S. ledermannii* may be locally abundant on Príncipe, its previously known distribution was limited to Cameroon and Nigeria; basis for inclusion of the species from Gabon by Symoens (1984) remains unknown. Both populations on Príncipe occur in moist leaf litter along streams in the shade of the surrounding moist evergreen forest at elevations of 10 and 150 m. Because this is the first report of Triuridaceae from both the nation of São Tomé and Príncipe and from any island in the Gulf of Guinea, a brief taxonomic overview of the family and *Sciaphila* on Príncipe is presented below.

Triuridaceae Gardner, Proc. Linn. Soc. London 1: 177. 1843

TYPE. *Triuris* Miers

Achlorophyllous mycotrophs (holosaprophytes), mostly perennial herbs. Stems erect from subterranean rhizomes, white, yellow, red, or purplish. Leaves scale-like, alternate. Inflorescence a terminal bracteate raceme. Flowers unisexual or bisexual, mostly actinomorphic, pedicellate. Perianth of 3–6 (–10) valvate tepals in single whorl. Bisexual flowers with 2–6 free stamens and numerous free carpels. Staminate flowers with 2-6 (-8) stamens, anthers 2–4-locular, pollen mostly inaperturate, exine reduced to gemmae. Carpellate flowers with 10 to many free carpels, each containing 1 (–2) basal, anatropous (or hemi-anatropous to campylotropous) ovule(s). Fruit an achene or follicle. Seed with copious endosperm.

A monocot family of 11 genera with 50 or more species occurring in tropical (and subtropical) regions worldwide. Although sometimes treated as related to the alismatid families (e.g., Cronquist 1981), recent molecular and morphological analyses show a closer affinity to an expanded Pandanales (Rudall and Bateman 2006). The anomalous flowers (or floral units) of Triuridaceae have been hypothesized to be either highly reduced inflorescences (pseudanthia) or highly modified flowers (see Rudall and Bateman 2006).

Sciaphila Blume, Bijdr. 10: 514. 1825

TYPE. *Sciaphila tenella* Blume

Plants monoecious or andromonoecious. Tepals (4–) 6 (–10), basally connate, internally papillate, apically sometimes bearded. Flowers unisexual or bisexual. Staminate flowers usually concentrated toward distal portion of raceme, stamens 2–6, epitepalous, filaments absent or less than 1 mm long, anthers (3–) 4-locular. Carpellate or bisexual flowers usually concentrated in proximal portion of raceme, carpels 10-80, style lateral. Fruit a follicle.

A genus in the tribe Sciaphileae Miers with 30–35 species occurring in tropical and subtropical regions worldwide, but with a center of species richness in the Indo-Malesian region of southeastern Asia. A single species in São Tomé and Príncipe, where it is known only from Príncipe.

Sciaphila ledermannii **Engl.**, Bot. Jahrb. 43:304, t. 1 (A-K, M-R). 1909. TYPE: CAMEROON. "Nkolebunde, an feuchten Stellen des Waldes mit wenig grossen Bäumen und viel Unterholz, ganz vereinzelt," Oct 1908, *C. Ledermann 745* (holotype: B). (Fig. 1)

Andromonecious perennial herbs to 2.5 dm tall; stems glabrous, usually simple, sometimes 1–2 branched, or less often with stems numerous and clustered (some with more than 2 branches) from a short subterranean rhizome or caudex, subterranean stems whitish, aerial stems bright red. Sterile scale-leaves 4–9, triangular-clasping, 2–5 mm long, 1.2–2 mm wide, glabrous, those above ground bright red. Inflorescence a terminal raceme, 3.5–13 cm long; rachis glabrous, bright red. Flower bearing scale-leaves (= bracts) triangular to lanceolate to ovate to elliptic to oblong, 1.3–3 mm long, 0.5–1 mm wide, glabrous. Pedicels ascending proximally and curved-reflexed distally,

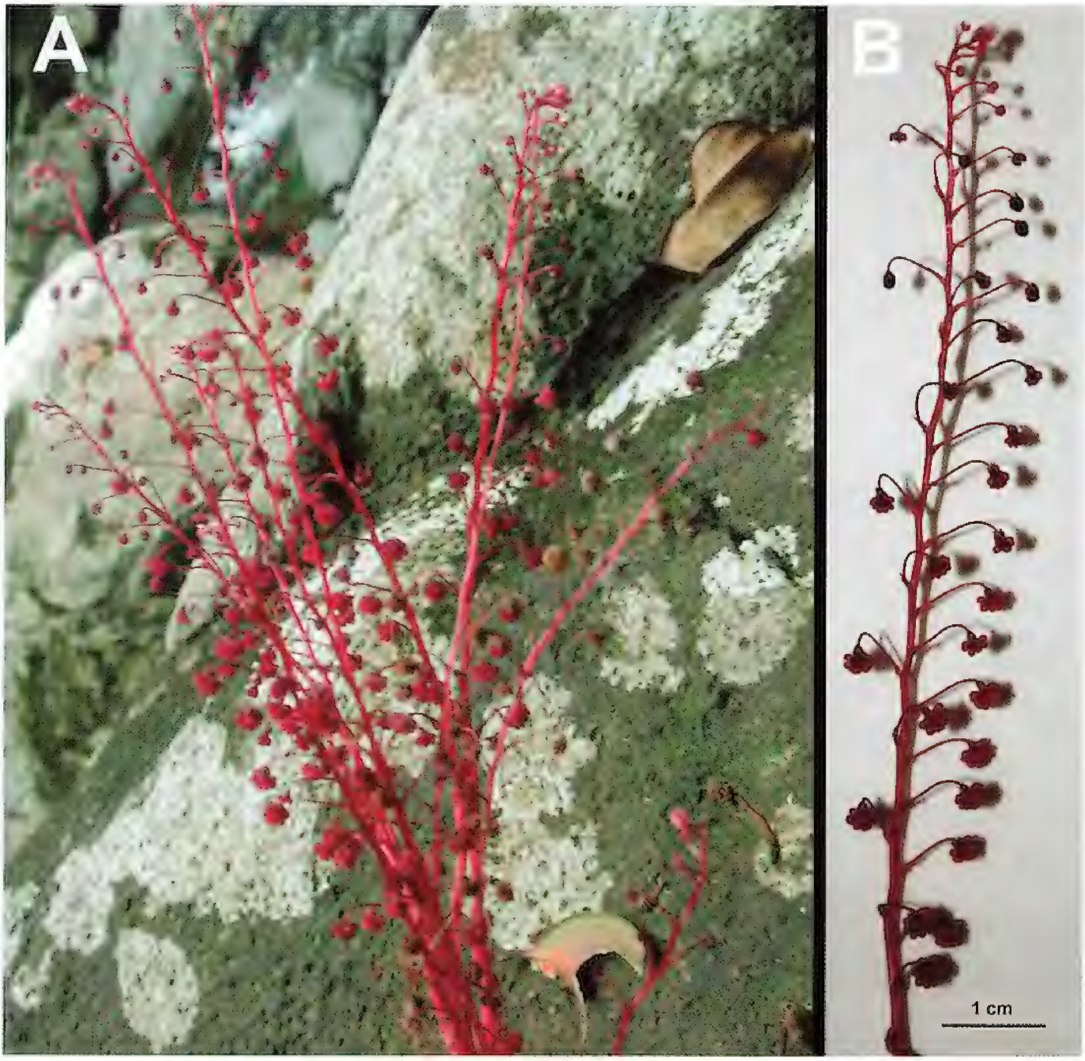

FIGURE 1. *Sciaphila ledermannii* (*Daniel et al. 11,699*) from Príncipe. A. Several individuals. B. Single plant.

(1–) 2-8.5 (–10) mm long, glabrous, bright red. Flowers 9-40 per raceme, mostly pendant, perianth reflexed during anthesis, 6-lobed, 0.9-1.4 mm long, lobes triangular to ovate, 0.6–1.2 mm long, 0.4–0.6 mm wide at base, apices pubescent with translucent and multi-celled trichomes to 0.7 mm long, trichomes deciduous and often not evident on older flowers. Staminate and bisexual flowers with 3 anthers, anthers 2-thecous, thecae ± explanate, broadly elliptic, 0.2 mm long. Bisexual (and carpellate?) flowers with 10–20 red carpels. Follicles ellipsoid to obovoid, 0.8–1.3 mm long, papillate. Seeds (Fig. 2A–C) broadly ellipsoid with ± tapered base (thus appearing ± oblacrymiform), 0.7–1 mm long, 0.4–0.7 mm wide, surface with 8 prominent longitudinal ribs and numerous less prominent transverse ridges.

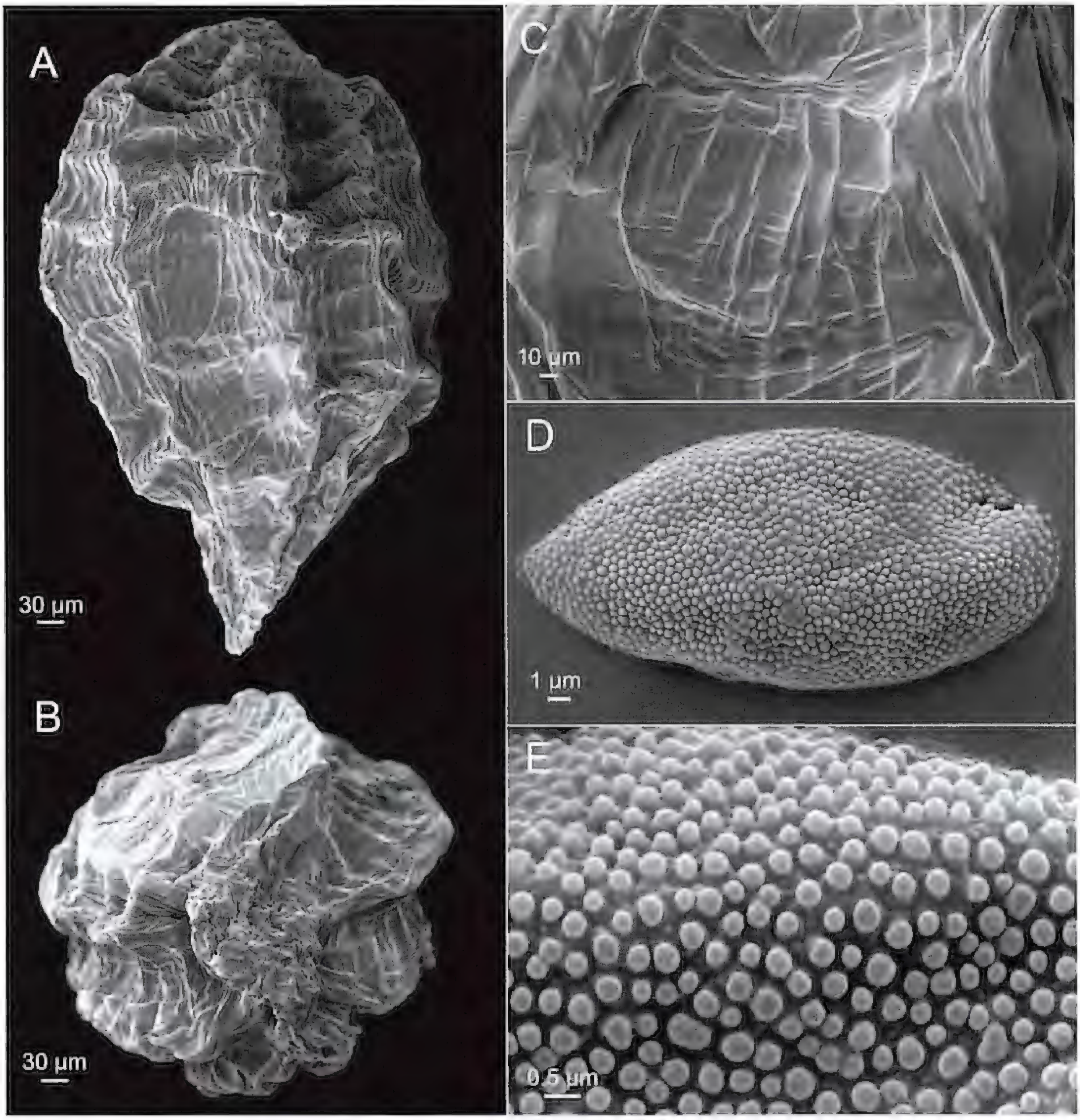

FIGURE 2. Scanning electron microscope images of seeds (*Daniel et al. 11,699*) and pollen (*Daniel et al. 11,716*) of *Sciaphila ledermannii* from Príncipe. A. Seed, lateral view. B. Seed, polar view. C. Seed surface. D. Pollen grain. E. Pollen surface with gemmate exine.

Illustrations.— Engler (1909: 305, fig. 1, A–K, M–R); Hepper (1968: 14, fig. 320); Symoens (1984:71, pl. 16).

Phenology.— Flowering: March; fruiting: March.

Distribution and habitats.— Known from Cameroon, Nigeria, and the Republic of São Tomé and Príncipe in the Gulf of Guinea region of western Africa; on Príncipe, plants occur in shade of undisturbed forests along streams at elevations from 10 to 150 m.

Specimens examined.— **São Tomé and Príncipe:** Príncipe: along Rio Papagaio ca. 2 km S of Bela Vista (SW of Santo Antonio), from hydroelectric dam site (01°36′15.6″N, 007°24′24.6″E) to ca. 0.5 km upstream (01°36′09.3″N, 007°24′22.1″E), 130–180 m, *T. Daniel et al. 11,699* (CAS, STPH); vicinity of mouth of Ribeira São Tomé and ca. 300 m upstream at southwestern end of island, between 01°33′36.5″N, 007°21′05.8″E and 01°33′42.8″N, 007°21′22″E, 0–50 m, *T. Daniel et al. 11,716* (CAS, STPH).

For plants from Príncipe, most of the flowers in an inflorescence are apparently bisexual, and these sometimes occur to the apex of the raceme. More typically, the terminal few flowers are staminate (i.e., lack carpels). Anthers or their remnants are present on many proximal flowers that bear fruits. It is unclear whether all of the proximal flowers have (or had) anthers or whether some are truly carpellate. Symoens (1984) likewise described plants from Cameroon as having inflorescences with the proximal flowers carpellate or bisexual and the distal flowers staminate, or sometimes with all the flowers bisexual.

Pollen of *Sciaphila ledermannii* (*Daniel et al. 11,716*, Fig. 2D, E) is generally collapsed and irregular in shape when observed with SEM. Like most other Triuridaceae, its pollen is inaperturate and covered with gemmae (Furness et al. 2002). Gemmae of *S. ledermannii* are relatively smooth, lacking the small protuberances observed in other taxa by Furness et al. (2002).

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I am grateful to the following organizations and individuals for facilitating my studies in São Tomé and Príncipe in 2010: California Academy of Sciences (Lewis and Elise Rose Memorial Fund), Société de Conservation et Développement, Jardim Botânico de Bom Sucesso and its herbarium (STPH), Ministry of Environment of the Republic of São Tomé and Príncipe, R. Drewes (Fig. 1A), E. Figueiredo, B. Loloumb, F. de Oliveira, N. Seligman, and J. Shevock.

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Two New Species of Nudibranch Mollusks From the Coast of California

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Two new species of nudibranchs are described from the coast of California. *Okenia felis*, from Monterey County, is white with six pairs of lateral appendages and a single medial papilla inserted into the notum on a broad base. This species is similar in appearance to *Okenia japonica* Baba, 1949, but it differs in consistent features of external, radular, and reproductive anatomy. *Flabellina goddardi*, from the intertidal zone of Santa Barbara County, is externally most similar to *F. pricei* (MacFarland, 1966) and *F. pellucida* (Alder and Hancock, 1843), all of which have ceratal rows that are inserted in elevated peduncles. However, both *F. pricei* and *F. pellucida* have smooth lateral teeth, while *F. goddardi* entirely lacks lateral teeth. The species is compared to the other 15 *Flabellina* that have been recorded from the Pacific coast of North America.

Key Words: California, Goniodorididae, Flabellinidae, *Okenia*, *Flabellina*, new species

The nudibranch fauna of the coast of California is diverse and varied. Behrens and Hermosillo (2005) listed 122 species of nudibranchs known from California, including two presently undescribed species. Gosliner (1996) also documented two new species of nudibranchs from deep water off the coast of southern California. Recently, two additional species have been collected from the California coast. The first taxon, a new species of *Okenia*, has been found from 37-40 m off Carmel, California. The species of eastern Pacific *Okenia* have been recently reviewed (Gosliner 1996; Camacho-García and Gosliner 2004; Gosliner & Bertsch, 2004). Nine species are known to occur from British Columbia to Costa Rica.

Millen and Hermosillo (2007) reviewed the fifteen species of *Flabellina* recorded from the eastern Pacific. A new species of *Flabellina* from the intertidal zone of Carpinteria, California that is clearly distinct from all other members of the Flabellinidae has recently been discovered.

The present paper describes these two new taxa and compares them to other known members of *Okenia* and *Flabellina*.

Species Descriptions

Family Goniodorididae Bergh, 1891

Genus *Okenia* Alder and Hancock, 1855

Okenia felis **Gosliner sp. nov.**
Figures 1A-B, 2A-D, 3A

Type material.— Holotype: CASIZ 174174, dissected, Pt. Lobos, Monterey County, California, 22 March 2009, 37–40 meter depth, collected by Robert and Alison Lee. Paratype: CASIZ

174175, one specimen, dissected. Pt. Lobos, Monterey County, California, 22 March 2009, 37–40 meter depth, collected by Robert and Alison Lee.

ETYMOLOGY.— *Okenia felis* is a noun from the Latin for cat indicating the appendages on notum that appear like cat whiskers. Also the collecting team that discovered this species, consisting of Robert and Allison Lee, John Heimann, and Clinton Bauder are known as "Team Kitty".

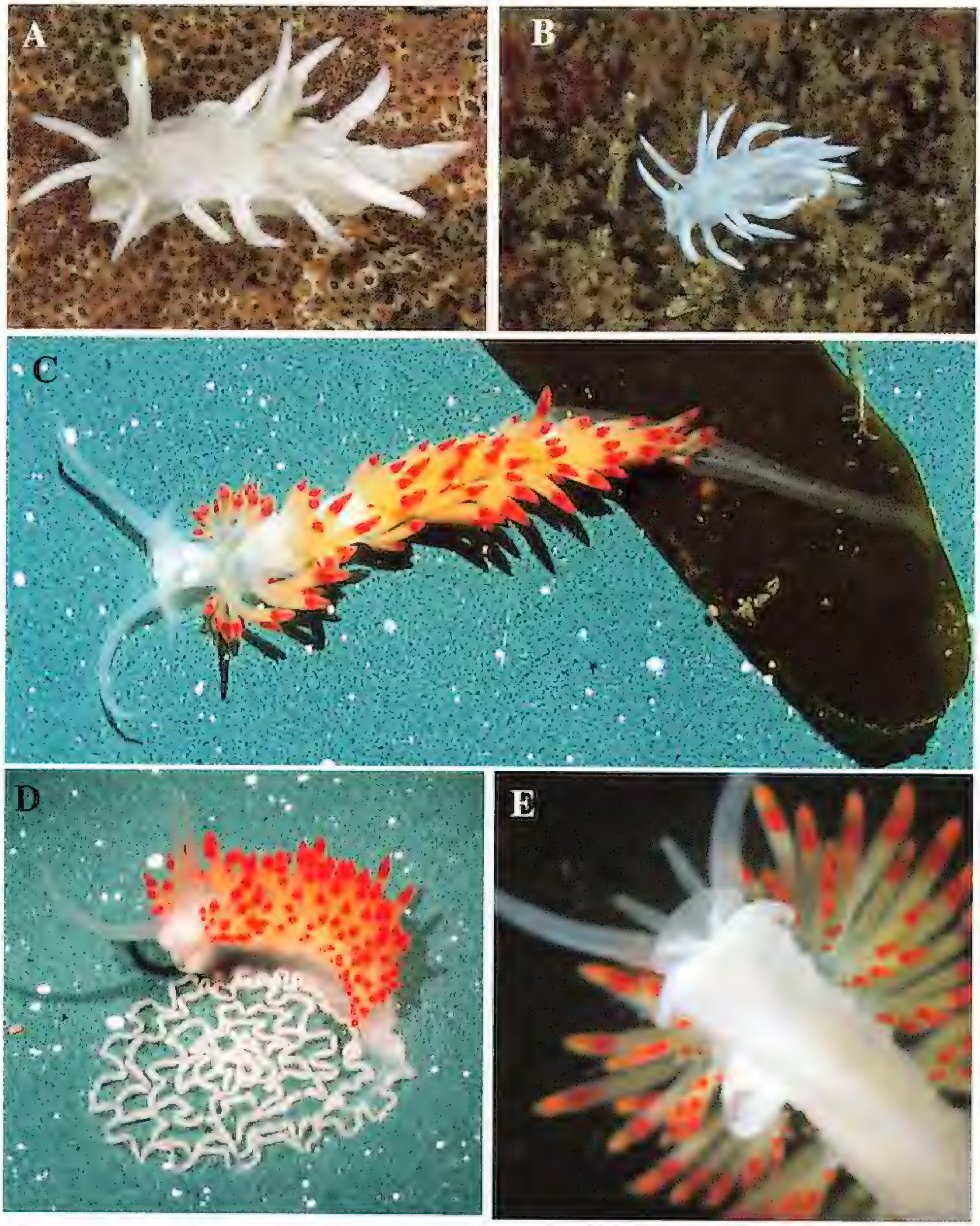

FIGURE 1. Living animals. A. *Okenia felis* sp. nov., Pt Lobos, Carmel, California. (Photo by Gary McDonald.) B. *Okenia felis* sp. nov., Pt Lobos, Carmel, California, *in situ*. (Photo by Rob Lee.) C. *Flabellina goddardi* sp. nov., whole animal, Carpinteria, California. (Photo by Jeff Goddard.) D. *Flabellina goddardi* sp. nov., animal with egg mass, Carpinteria, California. (Photo by Jeff Goddard.) E. *Flabellina goddardi* sp. nov., ventral view, Carpinteria, California. (Photo by Jeff Goddard.)

Distribution.— Known only from the type locality, Pt. Lobos, Carmel, California.

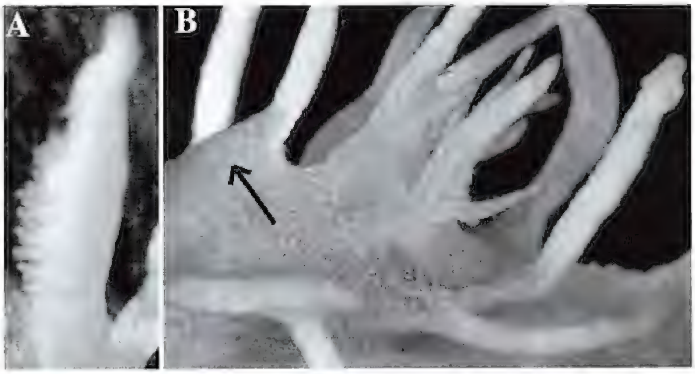

Figure 2. *Okenia* sp. nov. A. Detail of rhinophore. B. Detail of central papilla with base. (Photos by Gary McDonald.)

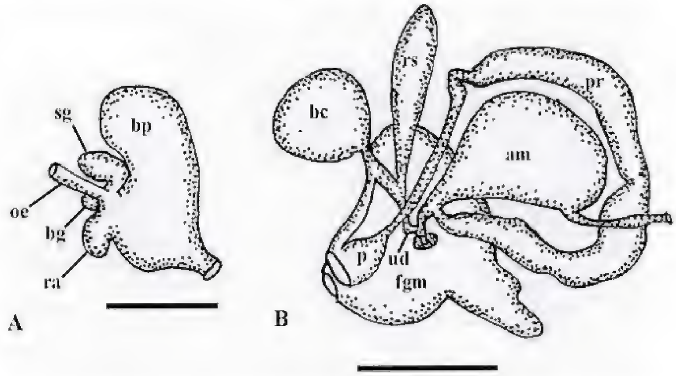

Figure 3. *Okenia felis* sp. nov. A. Oral tube, bg=buccal ganglion, bp=buccal pump, oe=oesophagus, ra=radular sac, sg=salivary gland, scale = 0.5 mm. B. Reproductive system, am=ampulla, bc=bursa copulatrix, fgm=female gland mass, p=penis, pr=prostate, rs=rectaculum seminis, ud=uterine duct, scale = 0.7 mm.

External morphology.— The living animals (Fig. 1A, B) are relatively small, reaching a maximum length of about 7–8 mm. The body is white with granules of opaque white scattered over the surface but more concentrated on the rhinophores and notal append-ages. The body is wide with a strong notal edge. Along the edges of the notum are six pairs of elongate notal papillae, each with a relatively acutely pointed apex. Just anterior to the gill is a single elongate, acutely pointed papilla that extends from an elongate thin membrane (Fig. 2B) that begins between the rhinophores and continues to the region immediately anterior to the gill. This base is elongate and sail-shaped. The rhinophores (Fig. 2A) are elongate with 21–23 lamellae on the posterior portion of the rhinophore. The lamellae begin at the base of the rhinophore and continue to the upper two-thirds of the rhinophore, leaving the apical third devoid of lamellae. The apex is elongate and rounded. The gill plume is opaque white, with 3 bipinnate branches. The foot is thickened anteriorly and there is pair of short, rounded tentacles on either side of the mouth.

Buccal armature.— The buccal mass is thick and muscular (Fig. 3A) with a rounded buccal pump directed posteriorly. Small, inconspicuous, oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. No obvious polygonal plates were visible (Fig. 4A). The cuticle expands as it enters the buccal pump. The radular formula is 20 × 1.1.0.1.1., in the holotype (Fig. 4B). The radula of the paratype was lost during preparation. The inner lateral teeth (Fig. 4C, E) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears about 19–23 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 4D) with a short cusp along the outer edge.

Reproductive system.— (Fig. 3B) The preampullary duct is elongate and thin and expands

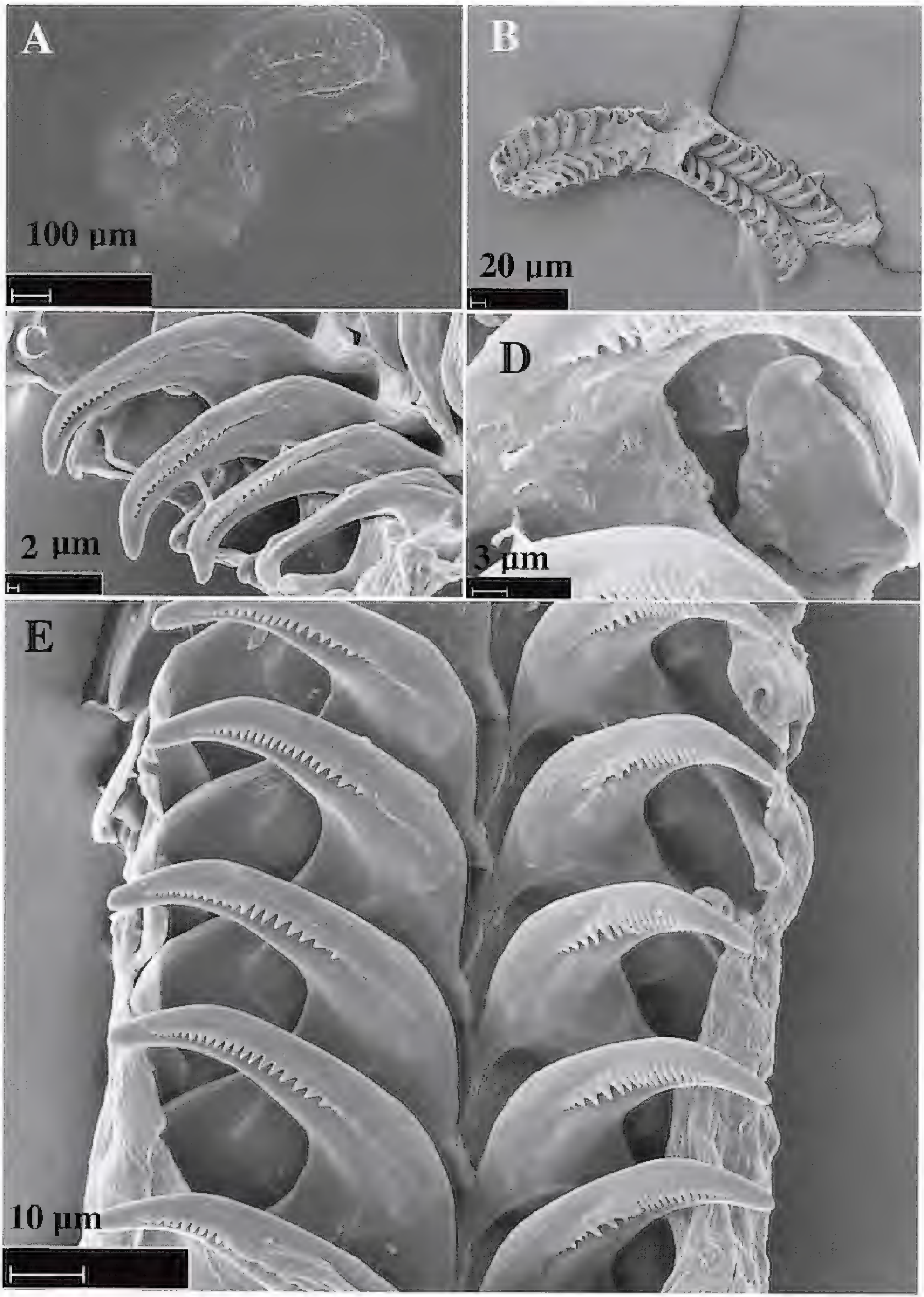

FIGURE 4. *Okenia felis* sp. nov. Scanning electron micrographs. A. Labial cuticle B. Entire radula. C. Inner lateral teeth. D. Outer lateral teeth. E. Half row of radular teeth.

into a globose ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of a single, undivided portion that surrounds the ampulla. The distal end of the prostatic segment narrows into an elongate, straight ejaculatory portion that terminates near at the distal end of the wide, short penis. There is no distinct penial papilla. Inside the distal end of the penis are penial spines. The vagina exits adjacent to the penis. It is narrow throughout its length. It connects directly to the spherical bursa copulatrix. The longer, club-shaped receptaculum seminis enters the uterine duct near the middle of the duct and then joins the short oviduct near its entrance to the albumen gland.

NATURAL HISTORY.— *Okenia felis* was observed to be locally abundant on a brown ctenostomatous bryozoan in deep water (37 to 40 meters) at Pt. Lobos, Carmel, California.

DISCUSSION.— The present species is most similar to *Okenia japonica* Baba, 1949, in that both species have a white body color with elongate lateral papillae along either side of the body and a single mid-dorsal papilla. There are some consistent differences between the species, which are summarized in Table 1. The most notable external difference is that *O. felis* has fewer pairs of lateral papillae than *O. japonica* and the central papilla of *O. felis* has a markedly wider base than that of *O. japonica*. Also, the rhinophoral lamellae are situated more basally in *O. felis* and are located more apically in *O. japonica*. Internally, the most pronounced differences are in the shape of the inner lateral teeth, where *O. felis* lacks the thick inner margin of the inner lateral teeth that is present in *O. japonica* (Gosliner 2004, fig. 7). Additionally, the receptaculum seminis of *O. felis* is elongate and club-shaped and inserts near the middle of the uterine duct as opposed to being rounded and inserting near the base of the bursa copulatrix in *O. japonica*. The vagina of *O. felis* is narrow throughout its length. The penis of *O. japonica* (Gosliner 2004, fig. 6C) is elongate and club-shaped and is separate from the rest of the vas deferens. In *O. felis*, the penis is short and wide and is situated at the terminal end of the vas deferens rather than adjacent to it.

Okenia academica Camacho-Garcia and Gosliner, 2004, from the tropical eastern Pacific also has a white body color, but has a much wider body and lacks the central dorsal papilla that is present in *O. felis*. It also has much shorter notal papillae and has reddish brown pigment on the body.

TABLE 1: Comparative data between *Okenia felis* and *O. japonica*.

	Okenia felis sp. nov	*Okenia japonica* Baba, 1949
Number of pairs of lateral papillae	6 per side	7–9 per side
Central notal papilla	With wide anterior base	With narrow base
Papillae apices	Acutely pointed	Rounded
Labial cuticle elements	Not readily visible	Large, prominent
Inner margin of inner lateral tooth	Not thickened	With thick margin
Receptaculum seminis size and shape	Elongate, club-shaped	Rounded, pyriform
Receptaculum insertion	Inserts near middle of uterine duct	Inserts at base of bursa copulatix
Vagina	Thin, short	Wide basally, elongate
Penis	Short, wide, terminal	Elongate, club-shaped, adjacent to vas deferens

There are also numerous other internal differences in the shape of the radular teeth and the arrangement of the reproductive organs. Another undescribed, deep-water species of *Okenia* was documented from the Santa Maria Basin of southern California (Gosliner 1996). This species has only 3-4 notal papillae on either side of the body and lacks a central papilla. It also has more elongate inner and outer lateral radular teeth.

Family Flabellinidae Bergh, 1889

Genus *Flabellina* Voigt, 1834

***Flabellina goddardi* Gosliner sp. nov.**
Figures 1D-E, 5- 7

Type material.— Holotype: CASIZ 182590, dissected, , Carpinteria State Park, Santa Barbara County, California, 8 May 2008, rocky intertidal, collected by Jeff Goddard.

Etymology.— *Flabellina goddardi* is named for friend and colleague, Jeff Goddard who found the only specimen of this distinctive species. Jeff is the consummate naturalist with superb powers of observation.

Distribution.— Known only from the type locality, Carpinteria State Park, Santa Barbara County, California.

External morphology.— The living animal (Fig. 1C–E, 5) is relatively small, reaching a length of about 15 mm. The body is a translucent white, with salmon-colored digestive gland within the cerata. The ceratal apices are bright yellowish orange with a subapical purple-orange band. The rhinophores are smooth, elongate and about 2/3 the length of the oral tentacles. The oral tentacles are thin and elongate, and taper to a thin apex. The anterior end of the head is notched and the anterior foot cornes are tentacular with apices directed laterally. The cerata are elongate and cylindrical throughout most of their length with a somewhat thinner base. The cnidosac is elongate and rounded (Fig. 5D). The cerata are arranged in distinct groups, which are on cushions elevated from the notum (Fig. 5B). There are 4 rows of cerata in the anterior, precardiac cluster with 4-9 cerata per row. The postcardiac cerata are arranged in seven distinct rows, with 1–10 cerata per row. The gonopore is situated on the right side of body, ventral to third and fourth ceratal rows. There is a large fleshy genital flap surrounding the gonopore (Fig. 5C). The pleuroproctic anus is situated in the middle of interhepatic space (Fig. 5A) and the nephroproct is immediately dorsal to the anus.

Buccal Armature.— The buccal mass is thick and muscular. On either side of the anterolateral portion of the buccal mass is a rounded, lobate oral gland (Fig. 6A) There is a pair of brown, coriaceous jaws (Fig. 7A). The masticatory border of each jaw bears a single row of about 12 triangular denticles that were visible under light microscopy but were not evident in the scanning electron micrograph (Fig. 7B). The uniseriate radula has a formula is 30 × 0.1.0, in the holotype. The rachidian teeth (Figs. 7C, D) are broad with a wide central cusp that is longer than the adjacent denticles. On either side of the central cusp are 7-8 elongate lateral denticles.

Reproductive system.— (Fig. 6B) The preampullary duct is elongate and thin and expands into curved ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. At this junction the large, pyriform receptaculum joins the common insertion via a long duct. The short oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. The oviduct exits adjacent to the curved bursa copulatrix. The bursa exits via a wide duct that has an even wider atrium. The prostatic portion of the vas deferens is wide and consists of a single, undivided portion

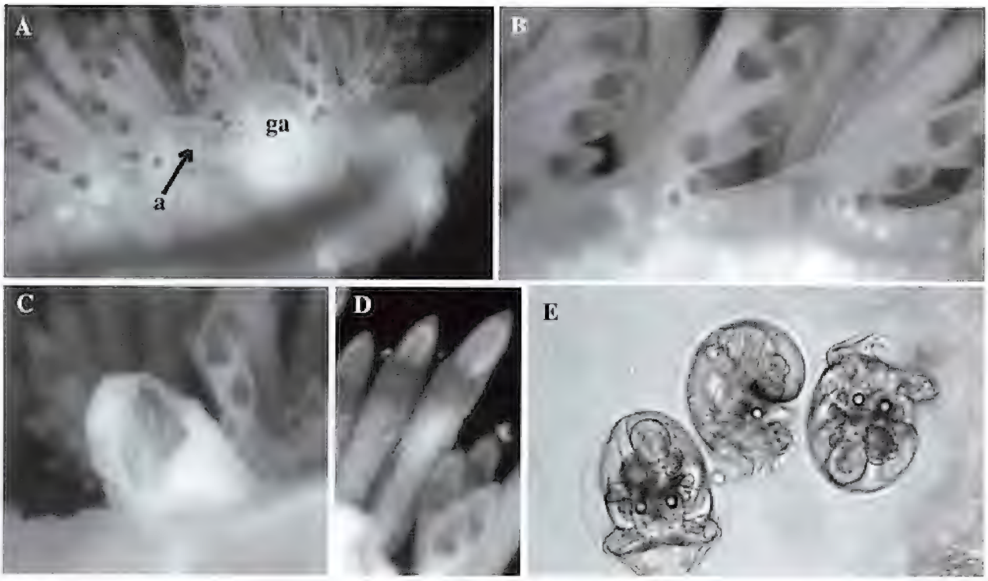

FIGURE 5. *Flabellina goddardi* sp. nov. A. Right lateral view of animal showing genital atrium and position of anus. B. View of ceratal clusters showing elevated peduncles. C. Genital atrium. D. Cerata showing digestive gland and cniosacs. E. Newly hatched veliger larvae. (Photos by Jeff Goddard.)

that is sausage-shaped. From the proximal end of the prostatic segment the narrow, short ejaculatory portion terminates near at the distal end of the wider, elongate penis. Thepenial papilla is conical and unarmed. Adjacent to the penial sac is a penial gland that is glandular throughout and is bifid at its distal end.

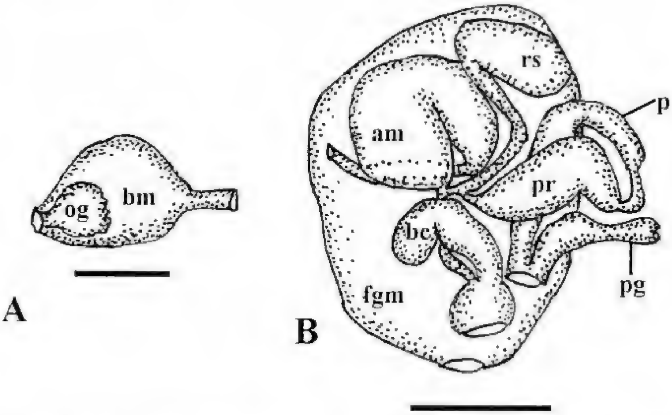

FIGURE 6. *Flabellina goddardi* sp. nov. A. Oral tube, bm= buccal mass, og=oral gland, scale = 0.4 mm. B. Reproductive system, am=ampulla, bc=bursa copulatrix, fgm=female gland mass, p=penis, pg=penial gland, pr=prostate, rs=rectaculum seminis, scale = 0.7 mm.

NATURAL HISTORY.— Little is known about the biology of this species. The single specimen was found in a tide pool at Carpinteria State Beach, Santa Barbara County, California. The single specimen produced a highly convoluted egg mass (Fig. 1D). From the egg mass, planktotrophic veliger larvae (Fig. 5E) emerged that possess a type 1 larval shell.

DISCUSSION.— The color pattern of *Flabellina goddardi* is unique among members of *Flabellina*. It is one of the only species that has orange and red-orange ceratal apices and subapical bands. The only other species that have a subapical purple band are *Flabellina marcusorum* Gosliner and Kuzirian, 1990, *F. rubrolineata* (O'Donoghue 1929), *F. exoptata* Gosliner and Willan, 1991, *F. delicata* Gosliner and Willan, 1991 and *F. riwo* Gosliner and Willan, 1991. The first four of these species have rhinophores with papillae on the posterior surface while *F. riwo* has perfoliate rhinophores. In contrast, *F. goddardi* has smooth rhinophores. All of the species mentioned above

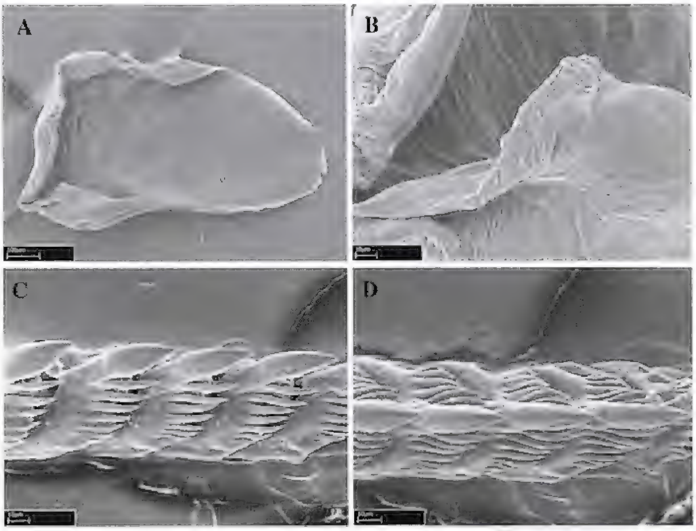

FIGURE 7. Flabellina goddardi sp. nov. A. Entire jaw. B. Masticatory margin. C. Lateral view of radular teeth. D. Dorsal view of radular teeth.

have highly digitate oral glands that extend into the notum, while *F. goddardi* has a pair of simple lobate glands located on the anterior portion of the buccal mass.

Flabellina goddardi bears some external resemblance to two previously described species, *Flabellina pellucida* (Alder and Hancock, 1843) and *F. pricei* (MacFarland, 1966), in that they have ceratal rows inserted on elevated cushions. *Flabellina pricei* has annulate rhinophores, while both *F. goddardi* and *F. pellucida* have smooth ones. The cerata of *F. pellucida* are more numerous and highly congested than in *F. goddardi*. Both *F. pricei* and *F. pellucida* have a radula with smooth lateral teeth (MacFarland 1966, pl. 65, fig. 13; Kuzirian 1979, fig. 7) while *F. goddardi* entirely lacks lateral teeth. The reproductive system of *F. pellucida* has not been described. The reproductive system of *F. pricei* (MacFarland 1966, pl. 66, fig. 8), differs from that of *F. goddardi* in that it lacks a receptaculum seminis or a penial gland.

In a description of a new species of *Flabellina* from Mexico, Millen and Hermosillo (2007) reviewed the systematics of the 15 species of *Flabellina* known from the Pacific coast of North America. Of these 15 species, only two species, *Flabellina amabilis* Hirano and Kuzirian, 1991, and *F. bertschi* Gosliner and Kuzirian, 1990, have smooth rhinophores as in *F. goddardi*. Both of these species have a triseriate radula with a lateral tooth on either side of the rachidian tooth, while the radula of *F. goddardi* is uniseriate. No other described species of *Flabellina* has a uniseriate radula. This derived feature raises questions as to whether this species should be placed in *Flabellina*. *Flabellina goddardi* shares several features with other flabellinids including the prescence of a pleuroproctic anus, presence of cerata on elevated cushions and a head with an anterior notch. In a preliminary molecular phylogeny based on the examination of the H3 nuclear gene and COI and 16S mitochondrial genes, *F. goddardi* was basal to a clade of *Flabellina* species but clearly distinct from the sympatric congeners, *F. iodinea* (Cooper, 1863), *F. trilineata* (O'Donoghue, 1921) and *F. pricei* (MacFarland, 1966). These data strongly suggest that *F. goddardi*, despite having a uniseriate radula, is most closely related to other species of *Flabellina*. Future molecular systematic studies of a wide range of *Flabellina* species are necessary to understand more precisely the systematic relationships and membership of the Flabellinidae.

ACKNOWLEDGMENTS

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Molecular Phylogenetics of Pacific *Nactus* (Squamata: Gekkota: Gekkonidae) and the Diphyly of Australian Species

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Eight recognized gecko species of the genus *Nactus* occur in landmasses bordering the tropical southwest Pacific, among them one widespread parthenogenetic species, *N. pelagicus*, and several additional very similar bisexual "*pelagicus* complex" species. We obtained and analyzed nuclear and mitochondrial DNA sequences from these eight species, as well as one undescribed *Nactus* species and several outgroups, in order to understand better the evolutionary history and biogeography of the genus. Phylogenetic analyses reveal that the three Australian species constitute two separate lineages. The ecologically and morphologically distinct Australian species *N. galgajuga* is found to be most closely related to the parapatric species *N. cheverti* of the *pelagicus* complex, whereas the other Australian member of the *pelagicus* complex (*N. eboracensis*) groups with an undescribed Papuan species. In addition, *N. multicarinatus* is confirmed as one of the parental species giving rise to *N. pelagicus*. New Guinean species of *Nactus* occur throughout the phylogeny, suggesting that *Nactus* originated there, with a single colonization of more distant Pacific islands and two colonizations of Australia.

KEY WORDS: Gekkonidae, *Nactus*, systematics, Australia, New Guinea, molecular phylogeny, biogeography

The gekkonid genus *Nactus* comprises a small radiation of 10 recognized extant species: five from islands of the southwest Pacific (including New Guinea), three from tropical north Queensland, Australia, and two from islets off Mauritius (Fig. 1). These species are terrestrial forest floor- or rock-dwellers lacking adhesive digital lamellae, distinguished from the externally similar genus *Cyrtodactylus* by the presence of the second ceratobranchial arch, fused nasals, and, in most species, rows of enlarged, multicarinate dorsal tubercles (Kluge 1983; Kraus 2005). In addition to named extant species, a third Mascarene species (*N. soniae*) is represented by subfossil material from Réunion (Arnold and Bour 2008), and multiple unnamed extant species are known (see below).

Within *Nactus* is a complex that includes *N. pelagicus* (Fig. 2) and several other morphologically similar, comparatively large-bodied (adult snout-vent length to 70 mm within complex; Zug and Moon 1995; Zug 1998) species. Formerly these were thought to represent a single species widespread in the Pacific. However, it has since been shown that *N. pelagicus* is a parthenogenetic species of probable hybrid origin restricted to eastern Melanesia (southern Vanuatu, New Caledonia, Fiji) and parts of Micronesia and Polynesia, whereas various sexually-reproducing species

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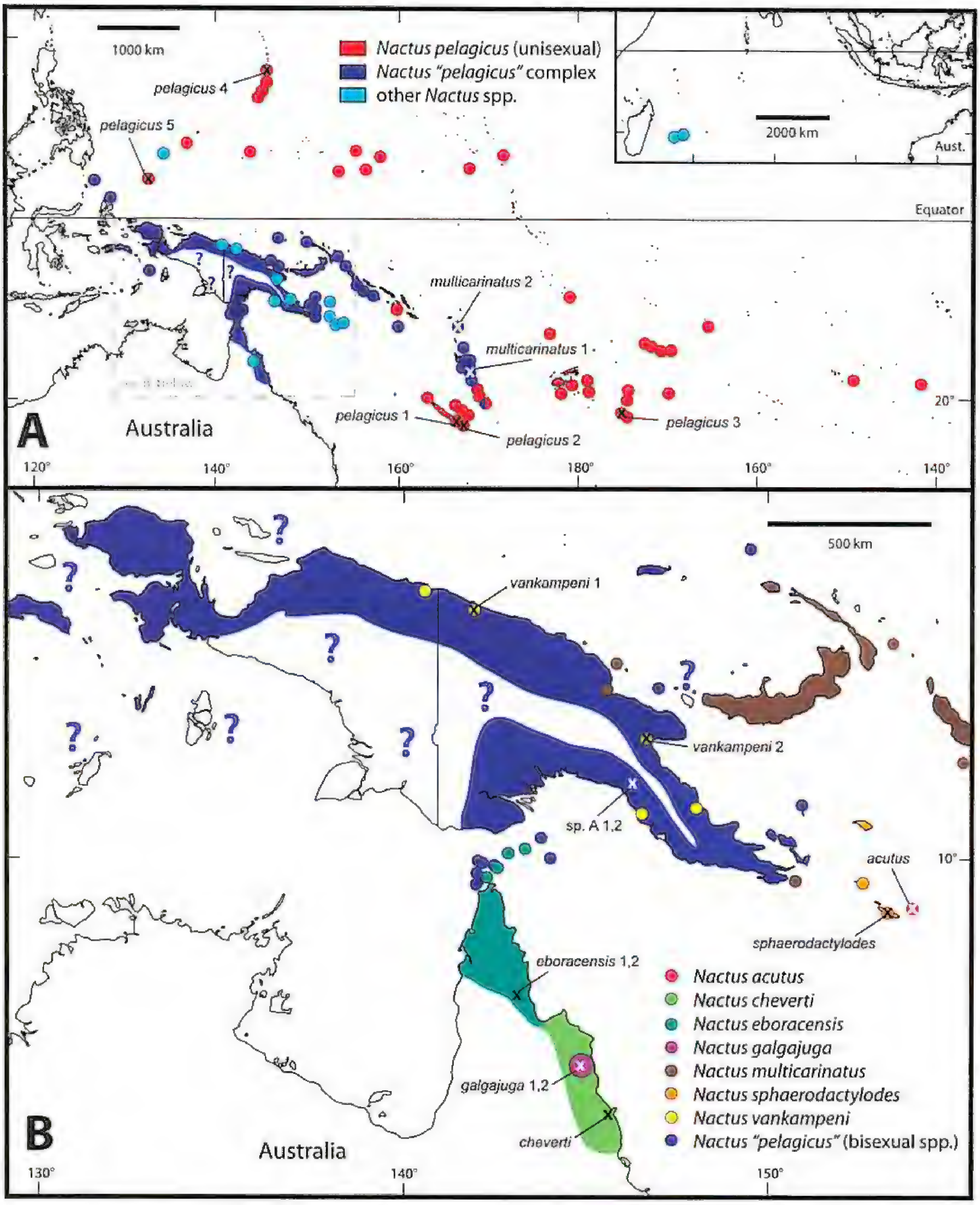

FIGURE 1. Distributions of *Nactus* species (A) Worldwide (main map: Pacific Ocean, inset: Indian Ocean) and (B) in New Guinea and Australia. Localities for samples used in this study are denoted by an (x), with *N. multicarinatus* and *N. pelagicus* mapped in (A), and other species mapped in (B). See Table 1 for specific localities. Distributions are based on Arnold and Jones (1994), Bauer and Henle (1994), Buden (2010), Crombie and Pregill (1999), Donnellan and Moritz (1995), Koch et al. (2009), Kraus (2005), Oliver et al. (2009), Zug (1998). Both the extent of distribution and specific identity of *Nactus* in central and eastern New Guinea and in the Moluccas are uncertain as indicated by the ? marks.

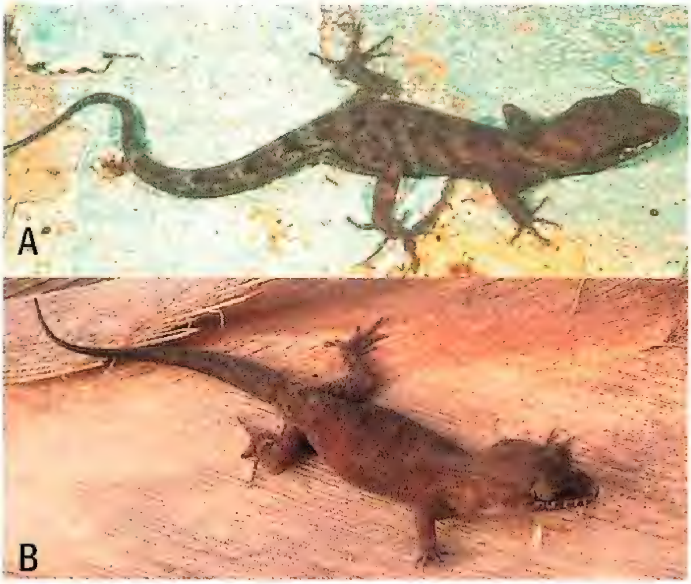

FIGURE 2. Life photographs of (A) *Nactus pelagicus* from Tao, Province Nord, New Caledonia [photo R.A. Sadlier] and (B) *N. multicarinatus* from Vanuatu [photo A. Hamilton]. Note the similarity between the unisexual *N. pelagicus* and its sexual parental form.

of the *pelagicus* complex occur elsewhere: *N. cheverti* and *N. eboracensis* in Australia (Fig. 3), *N. multicarinatus* in the Solomon Islands and northern Vanuatu (Fig. 2), and multiple undelimited species, usually cited as "*N. pelagicus*," in Palau, the Moluccas, and New Guinea (Fig. 1) (Kopstein 1926; Moritz 1987; Donnellan and Moritz 1995; Zug and Moon 1995; Zug 1998; Crombie and Pregill 1999; Oliver et al. 2009). A phenotypic male has also been collected from the Caroline Islands, but may represent a developmentally abnormal *N. pelagicus* (Buden 2010). At this time it is not clear how many species of bisexual "*pelagicus*" occur in New Guinea. Allozyme data identify three groups in Papua New Guinea, one of which represents a wider-ranging *N. multicarinatus* (Donnellan and Moritz 1995), while four forms have been identified based on morphology (Rösler et al. 2005), and an ongoing research program identifies at least five (G. Zug,

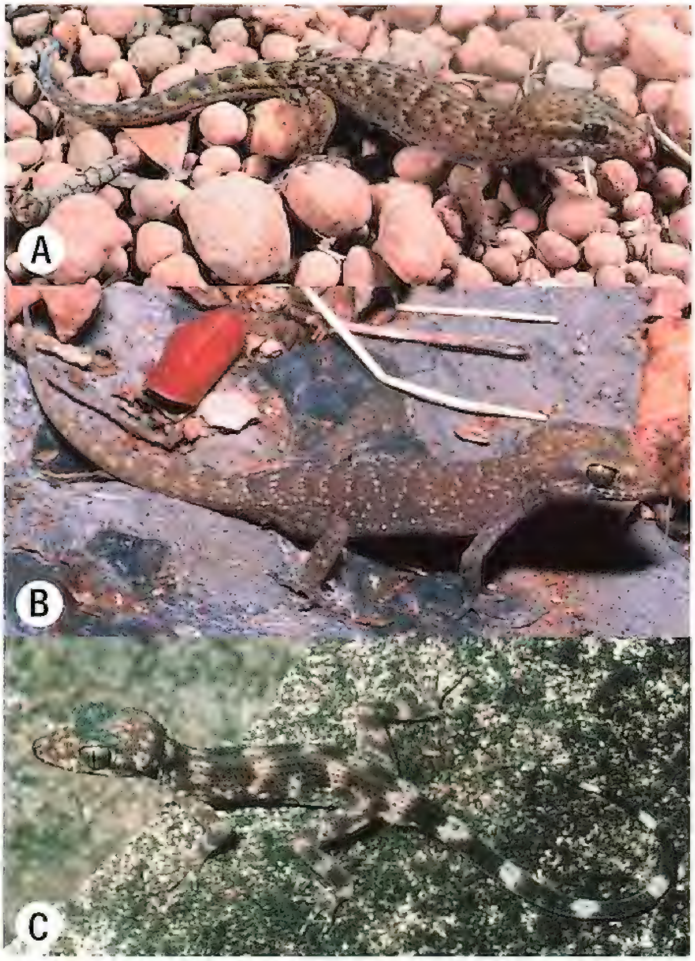

FIGURE 3. Life photographs of *Nactus* spp. from Queensland, Australia: (A) *N. eboracensis* (MS 621) from 64 km north of Aurukun, (B) *N. cheverti* (NV 184) from Chillagoe, and (C) *N. galgajuga* (NQ 321) from Black Mountain. Although morphologically similar, the former two species are not closely related. The highly autapomorphic *N. galgajuga* is the sister species of *N. cheverti*. Photos by Queensland Museum (A), and Steve Wilson (B and C), provided courtesy of Patrick Couper and Queensland Museum Image Collection.

pers. comm.). Several names are available for these bisexual "*pelagicus*," one of which is a subspecies endemic to the Kei Islands: *N.* "*pelagicus*" *undulatus* (Kopstein 1926). One Mauritian species, *N. serpeninsula* (including its subspecies, *N. serpeninsula durrellorum*; see Michels and Bauer 2004 for justification of emended name), has very similar morphological features to members of this complex, and has also been phylogenetically linked to *N. pelagicus* (Bullock et al. 1985; Arnold and Jones 1994); alternately, it has been proposed to form a monophyletic group with the other Mascarene species (Ulber and Gericke 1988). Although the members of the *N. pelagicus* complex were once considered conspecific, their monophyly has not been thoroughly tested, and relationships among species in the complex are not resolved. It is clear based on chromosomal and allozyme data, however, that *N. multicarinatus* does represent one progenitor of *N. pelagicus* (Moritz 1987; Donnellan and Moritz 1995).

There have been several published hypotheses of evolutionary relationships among *Nactus* species, but each has been based on data sets of limited character or taxon sampling. Donnellan and Moritz (1995) constructed a UPGMA phenogram of allozyme electrophoretic data that included multiple individuals of bisexual "*pelagicus*" from Australia, New Guinea, and the South Pacific. These individuals fell into four groups. Groups II and III (two New Guinea populations) were closest relatives, followed by Group I (equivalent to *N. cheverti*), with Group IV (equivalent to *N. multicarinatus*) being the most distant. In describing two new species, Kraus (2005) performed a parsimony analysis of morphological data to construct a phylogeny of all *Nactus* species. The results showed that *N. galgajuga* of Australia (Fig. 3C) and *N. coindemirensis* of Mauritius fell outside *Nactus*, with *galgajuga* in a polytomy with the outgroups and *coindemirensis* embedded within them. The *N. pelagicus* complex was recovered as monophyletic, with no variation among the species for the characters selected. However, the analysis employed only 23 characters (mostly external but some osteological) and did not include any bootstrap or other estimates of branch support. In contrast, Bullock et al. (1985) employed a limited morphological dataset to suggest a close relationship among *N. arnouxii* (= *N. pelagicus*), *N. galgajuga*, and *N. serpeninsula*. At the time of that study, no bisexual *pelagicus* complex species had yet been recognized. A monophyletic grouping of the Australian species of the *N. pelagicus* complex plus *N. galgajuga*, to the exclusion of other *pelagicus* group species, was proposed based on the shared presence of smooth subcaudal scales (Zug 1998). Likewise, DNA sequence data apparently does confirm that *N. coindemirensis* groups with other *Nactus*, although no phylogeny or explanation of its relationships to other *Nactus* speices has been published (Arnold and Bour 2008). Jackman et al. (2008) included several species of *Nactus* in phylogenies constructed using both mitochondrial and nuclear genes. The phylogenies included only *N. pelagicus sensu stricto* and New Guinean taxa, however, and many branches received low support. These analyses demonstrated a high degree of discordance between mitochondrial and nuclear data. In general, the nuclear gene phylogeny was most consistent with the morphological analysis of Kraus (2005), placing together *N. pelagicus* with a sexually-reproducing New Guinea "*pelagicus*" population and *N. acutus* with the similar *N. sphaerodactylodes*.

In order to understand better the relationships among the Pacific species of *Nactus*, we herein build on the molecular dataset of Jackman et al. (2008), including additional samples of *N. pelagicus*, as well as the previously-unsampled species *N. cheverti*, *N. eboracensis*, *N. galgajuga*, and *N. multicarinatus*. Our primary goals revolve around the Australian species: to confirm the placement of *N. galgajuga* in *Nactus*, to test the monophyly of the *N. pelagicus* species complex, and to determine whether the Australian species form a monophyletic assemblage, as suggested by Zug (1998), or if they constitute two or three independent lineages. If the species of the *N. pelagicus* complex are each others' closest relatives, it would suggest that at least *N. galgajuga* forms a separate lineage in Australia. In addition to these goals, the inclusion of multiple allopatric samples of *N. pelag-*

icus from New Caledonia in Melanesia, Tonga in Polynesia, and the Marianas Islands and Palau in Micronesia, along with *N. multicarinatus* samples, also allows us to confirm the origin of the parthenogenetic species *N. pelagicus*.

MATERIAL AND METHODS

Sequences were generated or obtained from GenBank for eight named and one undescribed species of *Nactus*, including multiple individuals of six species (Table 1, Fig. 1). Together, these data include all named extant species of *Nactus* with the exception of the two Mascarene species *N. coindemirensis* and *N. serpeninsula*. The samples labeled as *Nactus* sp. A, from Tekadu, Papua New Guinea, represent one of the bisexual species of New Guinea "*pelagicus*". Sequences from two species of *Heteronotia* and four of *Dixonius* were used as outgroups, based on previous work demonstrating these two genera represent the closest relatives of *Nactus* (Jackman et al. 2008). The data set consists of multiple mitochondrial and nuclear genes: the complete sequence of the mitochondrial NADH dehydrogenase subunit 2 (ND2; 1,035–1,041 bp), along with partial or complete sequences of 5 adjacent tRNAs (372–387 bp), plus partial exon sequences of the nuclear genes recombination activating gene 1 (RAG-1; 1,038 bp) and phosducin (PDC; 395 bp).

For generation of new sequences, genomic DNA was isolated from ethanol-preserved tissue samples using a Qiagen DNeasy tissue and blood kit under manufacturers' protocols. PCR was performed in 25 μL reactions, with primer sequences retrieved from the literature (Jackman et al., 2008). Standard reaction conditions included an initial denaturation at 95°C (2 min), followed by 32–34 cycles of denaturation at 95°C (35 s), annealing at 50°C (35 s), and extension at 72°C (initially 150 s, with 4 s added per cycle). Annealing temperature was lowered for poor-yielding samples. Purification of amplified PCR products was via AMPure magnetic bead system (Agencourt Bioscience). The sequencing reaction employed dye-terminator chemistry, with cycle sequencing followed by purification via the CleanSeq magnetic bead system (Agencourt Bioscience). Capillary electrophoresis and analysis were performed using an ABI 3700 sequencer. Resulting chromatograms were inspected by eye and compared against their reverse complements in BioEdit (Hall 1999) to detect call errors, followed by translation to check for premature stop codons. Sequences were then aligned using Clustal (Thompson et al. 1994), and manually corrected to take into account codon deletions and tRNA secondary structure.

Bayesian, likelihood, and parsimony methods were employed for phylogenetic analyses. Separate analyses were employed combining all data, nuclear genes only, and mitochondrial genes only. Neighbor-joining analyses were performed in MEGA 4 (Kumar et al. 2008) to confirm no significant conflict between the two nuclear genes prior to their concatenation. For the Bayesian and likelihood analyses, PhyML (Guindon and Gascuel 2003) and jModelTest 0.1 (Posada 2008) were used to estimate parameters for all standard models of evolution, with the Akaike Information Criterion (AIC) used to identify the best-fitting models of evolution. Based on the AIC, the GTR + I + Γ model was chosen for the combined analyses and GTR + Γ for the nuclear gene analyses. The TVM + I + Γ model was suggested for the mitochondrial analyses, but due to software limitations the similar GTR + I + Γ model was used instead. For all analyses, alignment gaps were treated as missing data, and pairwise deletion of sites was employed.

The Bayesian analyses were run in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). For each analysis, two parallel runs with three heated and one cold chain were run for 1,000,000 generations, with a sampling frequency of 100 generations per sample. The data were partitioned by gene (with all tRNAs pooled as a single gene). The first 2,000 samples (200,000 generations) were discarded as burnin for all analyses. The average standard deviation of split frequencies (all < 0.01) and

TABLE 1. Samples used in this study. Newly generated sequences include GenBank accession numbers HM997152–HM997187. Abbreviations are as follows: AMS = Australian Museum (Sydney), ASW = Alison Swindle Whiting field series, BPBM = Bernice P. Bishop Museum, CAS = California Academy of Sciences, FMNH = Field Museum of Natural History, LSHC = La Sierra Herpetology Collection (Riverside, CA), QM = Queensland Museum, USNM = United States National Museum, ZFMK = Zoologisches Forschungsmuseum Alexander Koenig. Numbers following species names correspond to localities mapped on Figure 1.

Species	ID number	Locality	GenBank Accession Numbers		
			ND2	RAG-1	PDC
Nactus pelagicus 1	CAS 229289	Mount Gouemba, Province Sud, New Caledonia	EU054291	EU054275	EU054259
Nactus pelagicus 2	CAS 203044	Ile des Pins, Province Sud, New Caledonia	EU054290	EU054274	EU054258
Nactus pelagicus 3	USNM 322160	1–4 km ENE Pangai, 'Eua Island, Tongatapu group, Tonga	HM997161	HM997173	HM997185
Nactus pelagicus 4	USNM 536071	Sarigan Island, Northern Marianas Islands, USA	HM997163	HM997175	HM997187
Nactus pelagicus 5	USNM 539365	Merir Island, Southwest Group, Palau	HM997162	HM997174	HM997186
Nactus multicarinatus 1	USNM 333894	Klem's Hill, ca. 3 km E. Mele Maat, Efate Island, Vanuatu	HM997159	HM997171	HM997183
Nactus multicarinatus 2	USNM 533297	vicinity of Ngandeli, Ngatado Island, Reef Islands, Temotu, Solomon Islands	HM997160	HM997172	HM997184
Nactus cheverti	USNM 561874	ca. 4 km SE Redlynch, Queensland, Australia	HM997154	HM997166	HM997178
Nactus galgajuga 1	USNM 561888	Black Mtn., ca. 20 km S Cooktown, Queensland, Australia	HM997158	HM997170	HM997182
Nactus galgajuga 2	QM 78303	Black Mountain, near Cooktown, Queensland, Australia	HM997157	HM997169	HM997181
Nactus eboracensis 1	USNM 561877	Paddy Shepard's Station, ca. 2 km S Coen, Queensland, Australia	HM997155	HM997167	HM997179
Nactus eboracensis 2	USNM 561880	Paddy Shepard's Station, ca. 2 km S Coen, Queensland, Australia	HM997156	HM997168	HM997180
Nactus sp. A 1	ASW 510	Lakekamu River basin, Tekadu, Morobe Province, Papua New Guinea	EU054292	EU054276	EU054260
Nactus sp. A 2	ASW 666	Lakekamu River basin, Tekadu, Morobe Province, Papua New Guinea	EU054294	EU054278	EU054262
Nactus acutus	BPBM 20755	Rossel Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea	EU054289	EU054273	EU054257
Nactus sphaerodactylodes	BPBM 20759	Sudest Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea	EU054293	EU054277	EU054261
Nactus vankampeni 1	BPBM 23365	Wewak, East Sepik Province, Papua New Guinea	EU054295	EU054279	EU054263
Nactus vankampeni 2	BPBM 18671	Mount Shungol, Morobe Province, Papua New Guinea	EU054296	EU054280	EU054264
Dixonius aaronbaueri	ZFMK 87274	Nui Chua National Park, Ninh Thuan Province, Vietnam	HM997152	HM997164	HM997176
Dixonius melanostictus	no number	Thailand (captive)	HM997153	HM997165	HM997177
Dixonius siamensis	LSHC 7328	Phnom Aural, Purset Province, Cambodia	EU054299	EU054283	EU054267
Dixonius vietnamensis	FMNH 263003	Keo Seima District, Mondolkiri Province, Cambodia	EU054297	EU054281	EU054265
Heteronotia binoei	AMS 159893	Limestone Caves, Ashford, New South Wales, Australia	EU054302	EU054286	EU054270
Heteronotia planiceps	AMS 140331	23.3 km NNW jct. of Tunnel Creed Rd. and Great Northern Hwy., Western Australia.	EU054300	EU054284	EU054268

potential scale reduction factors (all values approaching 1.000) were consulted to ensure that the chains ran for an adequate length of time. Branch support was assessed using posterior probabilities. The likelihood analyses were performed using RAxML 7.2.6 (Stamatakis 2006). The same partitions employed in the Bayesian analyses were used in the likelihood analyses. Ten independent searches were employed to find the most likely tree, and branch support for each analysis was assessed with 1,000 nonparametric bootstrap replicates. For the parsimony analyses, close neighbor interchange searches were implemented in MEGA 4 (Kumar et al. 2008), with 30 random addition replicates and 1,000 nonparametric bootstrap replicates for each dataset.

RESULTS

The final complete dataset measured 2,881 bp (1,041 bp ND2, 407 bp tRNAs, 395 bp PDC, 1,038 bp RAG-1). Of this, 1,109 sites were variable, and 809 were parsimony-informative. The nuclear dataset included 1,433 sites (318 variable, 212 parsimony-informative), while the mitochondrial dataset included 1,448 sites (791 variable, 597 parsimony-informative). In the combined parsimony analysis, six equally parsimonious trees were found, each requiring 2,814 steps. These equally parsimonious trees differ only regarding the interrelationships among *Nactus pelagicus* samples. The score of the best likelihood tree from 10 independent inferences was –ln L 16528.912326. For the nuclear parsimony analysis, 60 equally parsimonious trees of 423 steps were recovered. Again, most differences result from unresolved relationships among *N. pelagicus* samples, but a strict consensus also leaves two other branches unresolved (both of which receive low bootstrap support). The best tree from the likelihood analysis has a value of –ln L 4387.327357. The mitochondrial parsimony analysis recovered six equally parsimonious trees (2376 steps), with the strict consensus showing unresolved branching within *N. pelagicus*, plus one other unresolved branch. The best tree from the likelihood analysis had a score of –ln L 11869.961999.

Within each of the three data sets (combined, nuclear, and mitochondrial), Bayesian, likelihood, and parsimony analyses recovered nearly identical topologies, with the exception of a few poorly-supported basal branches that differ among the analytical methods (Fig. 4). As was expected based on the results of Jackman et al. (2008), there is a significant degree of phylogenetic discordance between the mitochondrial and nuclear data sets, which in turn negatively affects branch support values for the combined analysis. However, several relationships are strongly supported in all three data sets. With both nuclear and mitochondrial data, *Nactus pelagicus* samples from all parts of the species' range form a tightly-clustered group, with *N. multicarinatus* in turn receiving significant support (posterior probabilities = 1.0, bootstrap ≥ 95) with all tree-building methods as the closest relative of *N. pelagicus*. Two other species pairs also receive significant support for monophyly with combined, nuclear, and mitochondrial data: *N. cheverti* + *N. galgajuga* and *N. eboracensis* + *N.* sp. A.

Other relationships are recovered with relatively strong support with either mitochondrial or nuclear data, but not both (Fig. 5). As in Jackman et al. (2008), the mitochondrial analyses recover a well-supported pairing of *Nactus sphaerodactylodes* + *N. vankampeni* (Bayesian PP/ML bootstrap/MP bootstrap = 0.99/79/80). Additionally, *N. acutus* is placed as the closest relative of *N. eboracensis* + *N.* sp. A (support values = 0.95/54/43). In contrast, the nuclear gene analyses significantly support *N. cheverti* + *N. galgajuga* as closest relatives of *N. multicarinatus* + *N. pelagicus*, with moderate support (0.98/59/37) for *N. eboracensis* + *N.* sp. A in turn clustering with this grouping. Together, these six species represent the *N. pelagicus* species complex, with the addition of *N. galgajuga*. The same branching pattern of these six species also occurs in the combined analyses, with similar support values for both basal branches. The three New Guinea non-*pelagicus* complex species then form a basal grade within *Nactus*, with fairly low support for a *N. acutus* + *N. sphaerodactylodes* pairing in the nuclear analyses.

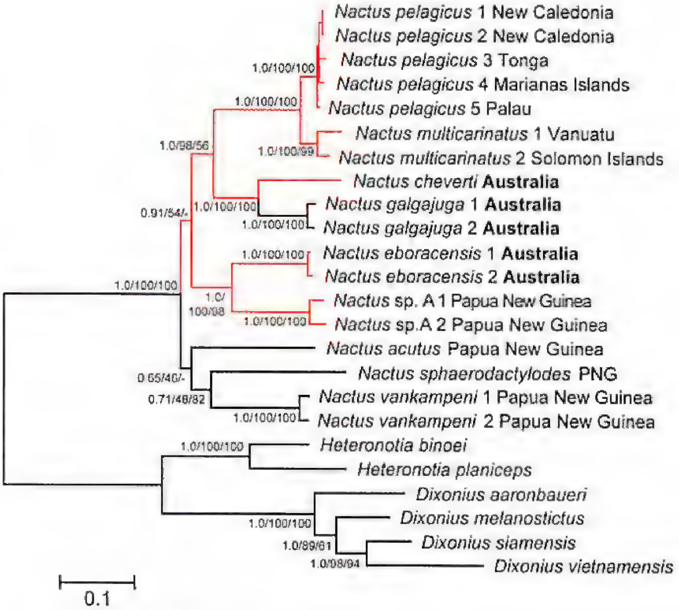
Nactus pelagicus 1 New Caledonia
Nactus pelagicus 2 New Caledonia
1.0/100/100
Nactus pelagicus 3 Tonga
Nactus pelagicus 4 Marianas Islands
1.0/100/100
Nactus pelagicus 5 Palau
Nactus multicarinatus 1 Vanuatu
1.0/98/56
1.0/100/99
Nactus multicarinatus 2 Solomon Islands
Nactus cheverti Australia
0.91/54/-
1.0/100/100
Nactus galgajuga 1 Australia
1.0/100/100
Nactus galgajuga 2 Australia
1.0/100/100
Nactus eboracensis 1 Australia
Nactus eboracensis 2 Australia
1.0/100/100
1.0/100/98
Nactus sp. A 1 Papua New Guinea
1.0/100/100
Nactus sp.A 2 Papua New Guinea
Nactus acutus Papua New Guinea
0.65/40/-
Nactus sphaerodactylodes PNG
0.71/48/82
Nactus vankampeni 1 Papua New Guinea
1.0/100/100
Nactus vankampeni 2 Papua New Guinea
1.0/100/100
Heteronotia binoei
Heteronotia planiceps
Dixonius aaronbaueri
1.0/100/100
Dixonius melanostictus
1.0/89/61
Dixonius siamensis
1.0/98/94
Dixonius vietnamensis
0.1

FIGURE 4. Bayesian phylogram of *Nactus*, rooted with *Heteronotia* and *Dixonius*, constructed with the combined nucleotide sequence dataset of the mitochondrial ND2 and adjacent tRNA genes plus the nuclear RAG-1 and PDC genes. Support values (Bayesian PP/ML bootstrap/MP bootstrap) are indicated at nodes. Branches leading to species traditionally considered part of the *N. pelagicus* complex are colored red.

DISCUSSION

As was previously noted by Jackman et al. (2008), the genus *Nactus* displays a high degree of discordance between the mitochondrial and nuclear sequence data. Of the two phylogenies, the nuclear gene phylogeny is much more in agreement with morphology and previous hypotheses of relationships, and is the hypothesis of relationships we favor. These data place together, on one hand, all members of the *N. pelagicus* complex, with the addition of the Australian species *N. galgajuga* (considered by Zug [1998] to be closely related to *N. cheverti* and *N. eboracensis*). On the other hand *N. acutus* and *N. sphaerodactylodes* group together, which share all character states in the morphological analysis of Kraus (2005) and have adjacent geographic ranges. The addition of several species does not change some of the interpretations of this gene conflict proposed by Jackman et al. (2008). Comparisons of the nuclear and mitochondrial phylogenies continue to suggest the low pairwise divergence of mitochondrial sequences in *N. vankampeni* could be the result of a recent selective sweep. Likewise, the association of *N. sphaerodactylodes* with *N. vankampeni* in the mitochondrial analysis and *N. acutus* in the nuclear analysis can still be explained as a result of mitochondrial introgression. However, the third conflict between mitochondrial and nuclear phylogenies described by Jackman et al. (2008), involving *N. pelagicus*, cannot be explained by that species' hybrid origin, as our data show that *N. multicarinatus* is closest to *N. pelagicus* in both nuclear and mitochondrial phylogenies. With the addition of new data, the placement of the *N. pelagicus* + *N. multicarinatus* clade in the mitochondrial phylogeny does not receive significant support, so this conflict may be most easily explained as a failure of the mitochondrial data to resolve deeper branches.

In our analyses, the phylogeny obtained using the combined dataset is much more similar to that using the nuclear data alone (Fig. 5), whereas in the analyses of Jackman et al. (2008), the mitochondrial data dominated the overall signal. Since the same gene regions were used in both studies, these results are seemingly contradictory. The four additional species included in this study appear to have broken relatively long branches leading to *N. pelagicus* and *N.* sp. A, especially in the case of the nuclear gene data. This has, in turn, had the effect of stabilizing the positions of *N. pelagicus* and *N.* sp. A in the combined analyses.

The close relationship observed between *Nactus pelagicus* and *N. multicarinatus* is not surprising, considering the chromosomal and allozyme evidence that *N. multicarinatus* represents one of the parental lineages giving rise to *N. pelagicus* (Moritz 1987; Donnellan and Moritz 1995). For the nuclear gene data, there are only three fixed nucleotide differences between the species over a span of 1,433 bases. However, the result that the two species also come out as sister taxa in mitochondrial analyses is somewhat surprising. Donnellan and Moritz (1995) proposed that *N. multicarinatus* (their Group IV) was the paternal ancestor of *N. pelagicus*, because of large differences observed between the two in mtDNA restriction fragment analyses. Because parthenogenetic species of lizard seem not to persist for long periods of time (Dawley and Bogart 1989, Vrijenhoek et al. 1989, Moritz 1991), their alleles should be genetically identical (or nearly so) to those of parental species. Our mitochondrial nucleotide sequence data suggest a much closer relationship between *N. pelagicus* and *N. multicarinatus* than the data of Donnellan and Moritz (1995), but the sampled mitochondrial alleles of *N. pelagicus* are still not identical or nested within those of *N. multicarinatus* (uncorrected pairwise divergence is approximately 0.060 between species, 0.045 within *N. multicarinatus*, and up to 0.013 within *N. pelagicus*). The level of sequence divergence within *Nactus pelagicus*, though small, is not trivial, and could suggest multiple origins of parthenogenic populations. However, no geographic pattern among *N. pelagicus* individuals is evident, with the two Micronesian (Marianas Islands + Palau) samples being no more closely related to each other than to the New Caledonian or Tongan samples. Thus, a single origin of parthenogenesis is most likely, although more samples of both *N. pelagicus* and *N. multicarinatus* are needed for confirmation. Assuming a fairly recent single origin of *N. pelag-*

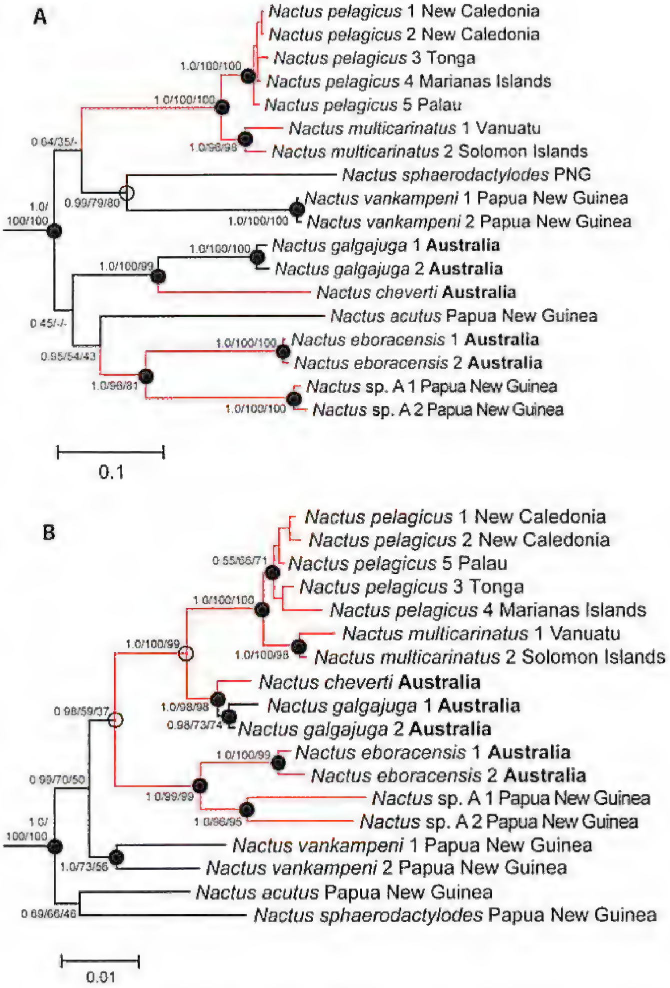
A
Nactus pelagicus 1 New Caledonia
Nactus pelagicus 2 New Caledonia
Nactus pelagicus 3 Tonga
Nactus pelagicus 4 Marianas Islands
Nactus pelagicus 5 Palau
Nactus multicarinatus 1 Vanuatu
Nactus multicarinatus 2 Solomon Islands
Nactus sphaerodactylodes PNG
Nactus vankampeni 1 Papua New Guinea
Nactus vankampeni 2 Papua New Guinea
Nactus galgajuga 1 Australia
Nactus galgajuga 2 Australia
Nactus cheverti Australia
Nactus acutus Papua New Guinea
Nactus eboracensis 1 Australia
Nactus eboracensis 2 Australia
Nactus sp. A 1 Papua New Guinea
Nactus sp. A 2 Papua New Guinea
1.0/100/100
1.0/100/100
0.64/35/-
1.0/98/98
0.99/79/80
1.0/
100/100
1.0/100/100
1.0/100/100
1.0/100/99
0.45/-/-
1.0/100/100
0.95/54/43
1.0/98/81
1.0/100/100
0.1
B
Nactus pelagicus 1 New Caledonia
Nactus pelagicus 2 New Caledonia
Nactus pelagicus 5 Palau
Nactus pelagicus 3 Tonga
Nactus pelagicus 4 Marianas Islands
Nactus multicarinatus 1 Vanuatu
Nactus multicarinatus 2 Solomon Islands
Nactus cheverti Australia
Nactus galgajuga 1 Australia
Nactus galgajuga 2 Australia
Nactus eboracensis 1 Australia
Nactus eboracensis 2 Australia
Nactus sp. A 1 Papua New Guinea
Nactus sp. A 2 Papua New Guinea
Nactus vankampeni 1 Papua New Guinea
Nactus vankampeni 2 Papua New Guinea
Nactus acutus Papua New Guinea
Nactus sphaerodactylodes Papua New Guinea
0.55/66/71
1.0/100/100
1.0/100/99
1.0/100/98
0.98/59/37
1.0/98/98
0.98/73/74
1.0/100/99
0.99/70/50
1.0/99/99
1.0/96/95
1.0/
100/100
1.0/73/56
0.69/66/46
0.01

FIGURE 5. Bayesian phylograms of *Nactus* constructed with (A) mitochondrial ND2 and tRNA sequences, and (B) nuclear RAG-1 and PDC sequences, illustrating conflicting branching patterns between the two data sets. Internal nodes appearing in all analyses (combined, nuclear, mitochondrial) are marked with filled circles, while nodes appearing in only the combined + mitochondrial (A) or combined + nuclear (B) analyses are marked with open circles. Outgroups are not depicted. Support values (Bayesian PP/ML bootstrap/MP bootstrap) are indicated at nodes. Branches leading to species traditionally considered part of the *N. pelagicus* complex are colored red.

icus, there are two possible interpretations of the data to explain the origin of *N. pelagicus*. *Nactus multicarinatus* may represent the maternal ancestor, with "*pelagicus*-type" ND2 alleles simply not present in our small sample or else lost to drift or selection. Alternately, *N. multicarinatus* may represent the paternal ancestor of *N. pelagicus*, with the unidentified maternal ancestor being an extinct or unsampled species of *Nactus* closely related to *N. multicarinatus*. Given that the pairwise ND2 sequence distances between *N. pelagicus* and *N. multicarinatus* are not much greater than those between our two *N. multicarinatus* samples, the former scenario, with *N. multicarinatus* as the maternal ancestor, seems more likely.

Even with the addition of conflicting mitochondrial data, the combined analysis recovers an expanded *Nactus pelagicus* complex with similar support values to that obtained using nuclear data only, which includes all three Australian species as well as both species from the Outer Melanesian Arc. Three sampled New Guinean species are basal to this complex, and several other New Guinean species belong to the *N. pelagicus* complex (one of which was sampled: *N.* sp. A) (Fig. 4). Although our combined and nuclear gene analyses place the Australian species *N. cheverti* + *N. galgajuga* with the Outer Melanesian species *N. multicarinatus* + *N. pelagicus*, allozyme data show the closest relatives of *N. cheverti* + *N. galgajuga* are actually undescribed bisexual New Guinea "*pelagicus*" (Groups II and III of Donnellan and Moritz) which were not included in our analyses (Donnellan and Moritz 1995). While we did not sample the Mascarene species, and they could potentially be basal to other *Nactus*, the direction of prevailing winds and surface currents in the tropical Indian Ocean strongly implies that dispersal must have occurred east to west (Austin and Arnold 2006). Taken together, the evidence supports New Guinea as the center of origin and diversification of *Nactus*, with multiple colonizations giving rise to the other extant species: two to Australia, one to the Outer Melanesian Arc (and beyond), one to Micronesia (Palau), and one or two to the Mascarenes. New Guinea has long been recognized as the source area for most of the Outer Melanesian herpetofauna (Allison 1996); it is also a source area for many tropical Australian genera. In addition to *Nactus*, the Australian gekkotans of the genera *Cyrtodactylus*, *Gehyra*, and *Lepidodactylus* are all probably derived from New Guinean sources (Allison 1996; Sistrom et al. 2009). Conversely, the only Australian-derived gekkotans to have colonized New Guinea are one genus and two species of morphologically-divergent legless lizards, *Lialis* (Kluge 1976).

Based on the combined and nuclear gene phylogenies, the morphotype exhibited by species of the *Nactus pelagicus* complex evolved early in the history of *Nactus*, and has remained largely unchanged in Australian, New Guinean, and Outer Melanesian species. However, *N. galgajuga* has diverged from the remaining species of the *N. pelagicus* complex morphologically: it is slender, with relatively longer, gangly limbs (Fig. 3C) and smooth rather than carinate dorsal and ventral scales (Ingram 1978, Kraus 2005). It has also diverged ecologically, occurring only in boulder fields rather than the forest floor habitat of most *N. pelagicus* complex species (Ingram 1978, Cogger 2000). The limb lengthening and loss of keeling exhibited by *N. galgajuga* may represent adaptations to its boulder-field habitat; other rock-dwelling lizards exhibit longer hindlimbs and dorsoventral flattening as compared to close relatives (Couper et al. 1993, Vitt et al. 1997, Revell et al. 2007, Goodman et al. 2008).

There are no fossils that can be used to calibrate a molecular clock within *Nactus*. Rough times of divergence can be estimated, though, for some key nodes by applying an ND2 pairwise divergence rate of 1.3% per million years, which approximates rates observed in a variety of squamates, including geckos (Macey et al. 1998; Macey et al. 1999; Guicking et al. 2006). Applying this rate, the divergence between *N. cheverti* and *N. galgajuga* occurred about 11 Ma, that between *N. eboracensis* and *N.* sp. A occurred about 11.5 Ma, and divergences among sampled *N. pelagicus* individuals occurred within the last million years. The recent divergence among *N. pelagicus* individuals post-dates the final emergence of the Solomon Islands 11 Ma and Vanuatu 2 Ma (Kroenke and Rodda 1984; Macfarlane et al. 1988; Hamilton et al. 2009). *Nactus pelagicus* and *N. multicarinatus* populations are sympatric on both archipelagoes, so assuming *N. pelagicus* still occurs at its point of origin, either could be the location of the original hybridization giving rise to *N. pelagicus*. The longer emergent history of the Solomon Islands, coupled with its location closer to the center of *Nactus* diversity in New Guinea, however, suggests those islands as the more likely point of hybridization. Donnellan and Moritz (1995) suggested that the tectonic evolution of Melanesia, particularly New Guinea, may have led to vicariant divergences among *N. pelagicus* complex species. We cannot comment on the relative likelihood of vicariance vs. dispersal in New Guinea, as we only included a single New Guinean species of the *N. pelagicus* complex in our study.

Within Australia, *Nactus eboracensis* is restricted to the northern Cape York area of endemism, whereas *N. cheverti* is endemic to the southern Cape York Peninsula, from Melville Peninsula south to the Atherton Tablelands, and *N. galgajuga* to the Black Mountains, south of Cooktown (Cracraft 1991; Zug 1998). Southern Cape York and Atherton Tableland endemics often have closest relatives or conspecific populations in New Guinea without close relatives distributed in the northern Cape York Peninsula, so it is not particularly surprising that the closest relatives of *N. cheverti* and *N. galgajuga* occur in New Guinea rather than in Australia. However, most of these many Atherton + New Guinea clades, including examples such as numerous diverse plant genera (*Stockwellia* + *Eucalyptopsis*, *Thaleropia*, *Telopea*, *Alloxylon*; Crisp et al. 1995; Ladiges et al. 2003), agamid lizards (*Hypsilurus*; Schulte et al. 2003), and tree kangaroos (*Dendrolagus*; Williams 2006), are absent in the northern Cape York because of habitat restrictions; they are rainforest specialists. Australian *Nactus* are not rainforest-restricted; instead, they occur in a variety of forest and woodland habitats (Cogger 2000; Williams 2006). Thus, it is probably competitive interaction between *N. eboracensis* and *N. cheverti*, rather than biogeographic history, that has determined the current ranges of the two species. Since *N. cheverti* and *N. galgajuga* have speciated within Australia (about 11 Ma) and are farther from New Guinea source populations, the ancestor of these species may have been the first *Nactus* to colonize Australia. *Nactus eboracensis* would have colonized from New Guinea later (after 11.5 Ma), and divided tropical north Queensland with *N. cheverti*. Southern New Guinea is part of the Australian Plate, and land connections facilitating faunal exchange between New Guinea and Australia have been present intermittently during periods of low sea level throughout the Neogene (Hall 1998, 2001). The presence of *Nactus* on many distant oceanic islands demonstrates the overwater dispersal ability of these geckos, however, and shows that the two colonizations of Australia need not have occured during a period of lowered sea level.

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Zooxanthellae in Ellisellid Gorgonians of the Philippines

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The common name "sea whip" applies to a variety of unbranched whip-like corals including the black corals *Cirripathes* and *Stichopathes*, the gorgonians *Viminella* and *Junceella*, and the sea pens *Halipteris*, *Funiculina*, and *Distichoptilum*. The symbiotic relationship between unicellular dinoflagellates (known as zooxanthellae) and coral reef octocorals almost always occurs in all species within a given genus. The few exceptions include *Virgularia*, *Cavernularia*, and *Pseudopterogorgia*. All ellisellid gorgonians have been previously recorded as a zooxanthellate (Fabricius and Alderslade 2001), but a zooxanthellate form was previously suspected in the genus *Junceella* by Sprung (1999).

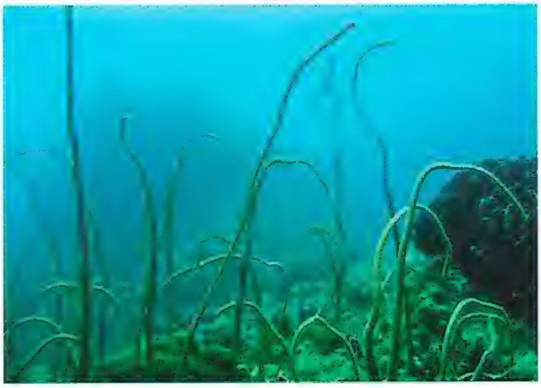

FIGURE 1. A dense aggregation of sea whips, Luzon, Philippines, 12 m depth.

Staff of the Steinhart Aquarium, California Academy of Sciences, collected five specimens of *Junceella fragilis* (Ridley 1884) at a depth of 12 m from Maricaban Island, Luzon (13°41′12.02″N, 120°49′38.01″E) in May 2010 (Fig. 1). On closer observation it became apparent that the brown polyp coloration might be due to the presence of zooxanthellae (Fig. 2), which was confirmed by microscopic examination of an excised polyp (Fig. 3). This validates the report of a zooxanthellate in *Junceella* (Oppen et al. 2005) and underscores the importance of working with live material when describing species characteristics.

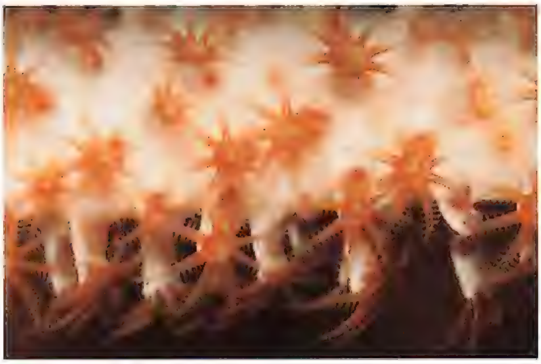

FIGURE 2. Brown, extended polyps of *Junceella fragilis*.

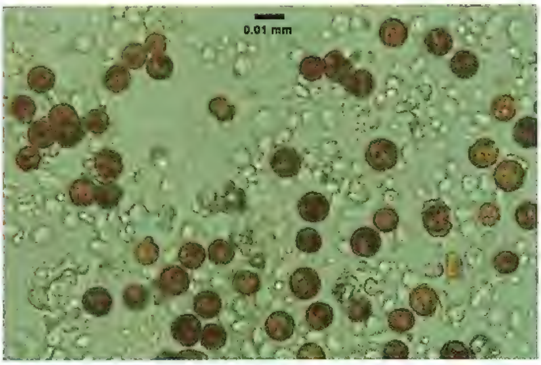

FIGURE 3. Zooxanthellae from polyps of *Junceella fragilis*.

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Compiled by Alan E. Leviton and Michele L. Aldrich

(New taxa are in **boldface** type)

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